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# THE DEHISCENCE OF ANTHERS BY APICAL PORES.

BY J. ARTHUR HARRIS.

## INTRODUCTION.

### HISTORY OF THE PRESENT INVESTIGATION.

During the summer of 1901, I became much interested in the pollination of *Solanum* and *Cassia* and, assisted by a student, published a paper giving the results of our investigations. At the time of the preparation of that paper, I was fully aware of a number of points meriting further field study and especially comparison with similar forms in other genera, and, upon taking up my work at the Missouri Botanical Garden, was glad to avail myself of the facilities offered by the herbarium and library for a comparison of the floral structures of other species of these large genera and for the accumulation of notes on some analogous types of flowers in other families.

While working on *Solanum* and *Cassia*, I was impressed by the close resemblance of the floral constitution of these systematically widely separated genera and by the similarity of their ecological relations. My interest was deepened when I observed that the same close agreement in the structure and frequently in the ecology of apically dehiscent forms is to be found in other families. Later, there came the question whether the great differentiation of *Solanum*, *Cassia* and the Melastomataceae in South America and the occurrence there of several smaller genera with apically dehiscent anthers might be significant. Obviously the question could be answered only by a comparative and statistical study of all genera and species showing dehiscence by apical pores, and the collection of data for

this purpose was immediately begun by examining Engler and Prantl's *Die Natürlichen Pflanzenfamilien*, Bentham and Hooker's *Genera Plantarum* and several of the more important floras, for the purpose of preparing a descriptive list of all forms in which the anthers have been described as opening by apical pores. This was intended to serve as a foundation for structural comparisons, and so far as might be possible, for a comparative treatment of the floral ecology of these forms.

The data secured and the conclusions which they seemed to indicate proved highly interesting and were presented in April, 1903, to the Faculty of Washington University as a thesis for the degree of Doctor of Philosophy. Since that time I have been able to secure a large amount of valuable material for study and have devoted much of my time which has been available for research to this problem. My manuscript has grown so large that it is inadvisable to publish it in full at present, especially since I have in hand further studies which I hope will add materially to its value but which cannot be completed for some months. It seems best to present an abstract outlining the problem and giving the essential points in the conclusions which seem justified by the comparisons so far carried out, with a much condensed statement of the data upon which they are based. The detailed treatment of the subject is being increased by structural, comparative, and ecological studies, and I hope to publish it in full, possibly with discussions of other floral types, at some future time.

I wish to avail myself of this opportunity to express my obligation to several gentlemen who have had the kindness to send material from their herbaria to the Missouri Botanical Garden for my use. These are: Dr. F. Kurtz, Universidad Nacional, Cordoba, Argentina; Dr. R. A. Philippi, Museo Nacional, Santiago de Chile; Dr. W. R. Guilfoyle, Botanic and Domain Gardens, Melbourne, Australia; Dr. J. M. Wood, Durban, Natal; Dr.

J. C. Willis, Royal Botanic Gardens, Ceylon; Dr. M. Treub, Jardin Botanique, Buitenzorg; Dr. J. H. Maiden, Government Botanist, Sydney, N. S. W.; Dr. I. Urban, Königlicher botanischer Garten und Museum, Berlin; Dr. T. Durand, Jardin Botanique de l'État, Bruxelles; and Dr. N. L. Britton, New York Botanical Garden.

This material, which was asked for only after the most of the data for this paper had been gathered and classified, has been consulted in the preparation of these pages but is being used mainly for a histological investigation of these types of anthers, and so my future memoir will owe even more to their generosity than the present one, which is very largely a library contribution. Perhaps nowhere else could this paper have been prepared so easily as at the library of the Missouri Botanical Garden, with its large collections of living and preserved plants also accessible for consultation, and I wish to express my gratitude to the Director, Dr. William Trelease, not only for access to these facilities, but for the most generous conditions under which I have used them while connected with the Garden and with Washington University. For several months Mr. Dean H. Rose has assisted me in this and in other research work, and while the most of his time has been given to phases of the subject which will be treated later, I wish to express in advance my hearty appreciation of the earnest and efficient service he has given me. My sister, Miss Nellie L. Harris, has been of great help to me in the preparation of the statistical portions of the paper.

#### EARLIER INVESTIGATIONS.

That in a comparatively limited number of Phanerogams, the pollen is shed through terminal pores instead of longitudinal slits is a fact of general knowledge which has been utilized in the characterization of families, genera, and species.

The method of the shedding of the pollen in the Angiosperms is a subject very briefly treated in the general works on morphology and physiology. Goebel in his *Organographie* calls attention to the obscure nature of many points in this phenomenon, and Coulter and Chamberlain in their recent work on the morphology of Angiosperms speak of the need of a thorough investigation of the subject, especially from the developmental point of view. Most general works treat this point with the same or greater brevity and need not be mentioned separately.

Histologically, anthers have been investigated and their minute anatomy interpreted more or less satisfactorily by several writers, among whom may be mentioned Mohl, Purkinje, Schrodt, Leclerc du Sablon, Chatin, and Steinbrinck.

So far as I am aware, no special treatment of the apically dehiscent anther has been attempted from a morphological, histological or ecological point of view.

#### PURPOSE OF INVESTIGATION AND SCOPE OF PRESENT PAPER.

My purpose in undertaking the present investigation was threefold: 1. The compilation of a systematically arranged descriptive list of genera or species showing dehiscence by pores, for use in future biological work. 2. The demonstration of any similarity of structure in apically dehiscent forms of different systematic affinities or the existence of possible correlative modifications in the parts of the flowers showing this method of dehiscence, if such exist. 3. The establishment or the refutation of the hypothesis that the flora of certain of the main divisions of the earth's surface is richer in apically dehiscent forms than that of others.

These three purposes were quite satisfactorily accomplished in the spring of 1903. During the time which has elapsed since the writing of my first manuscript I have added practically no new genera or species to my list. I

have, however, been able to supplement my descriptive data very materially by a comparison of the rich materials generously supplied by the directors and curators of botanical gardens and herbaria in various parts of the world. I have also been able to carry out several detailed and time-consuming comparisons between the apically and the longitudinally dehiscent members of the several families in which dehiscence by apical pores has been described. This I did to determine whether the type of floral structure which is repeated with such uniformity by the apically dehiscent members of several little related families, is of frequent occurrence in these families, or whether the form of the anthers and the general habit characteristic of these apically dehiscent genera or species are aberrant in the systematic groups to which they have been assigned by taxonomists.

I have been able to satisfy myself more fully concerning the distribution of forms by tabulating according to arbitrarily limited floristic regions the distribution of all the genera of Phanerogams. The distributional phase of the problem is still far from satisfactory and must necessarily long remain so. These tabulations, however, confirm my early impression of the greater richness of the flora of some regions in species with apically dehiscent anthers.

Floral structures are to be fully interpreted only through a knowledge of their ecological relations, past and present. I have been able to compile a considerable series of such data bearing upon the forms under consideration and while these, with the few observations which I have been able to make, represent only a beginning, they seem to justify some very suggestive hypotheses for further investigation.

Convinced that the great systematic differentiation attained by the Apidae in South America might have a significant bearing upon the problem, I have tabulated the distribution of this family, and by way of comparison, that of all families of the Hymenoptera.

It is a pleasure to say that the work which has been done since the spring of 1904 has not materially modified the conclusions then reached, but has added more convincing evidence from many sides.

In this place I shall not give a systematically arranged list of the forms I have considered. This, with the necessary bibliographic citations and descriptive text and illustrations, would require far more space than is available. I shall rather divide the former into groups or types and describe these briefly, mentioning, when desirable, the names of the genera assigned to the particular types, with their geographical distribution, and comparing their structure briefly with the forms to which they are systematically related. It is to be understood that these groups or types are not sharply defined categories, but transgressive assemblages. The justification for the division of the material into these groups or types is found in the fact that the majority of the species do fall clearly into one or the other of the groups, while those which represent transitions or are quite aberrant in structure are much rarer. These groups are to be regarded as tentative, and, while for the most part natural, they are established primarily for the convenience of the present discussion. Their great justification is to be found in the convenience of treatment and interpretation which does result from their use.

Four of these types I shall consider very briefly, merely describing in general terms their differential characters. The fifth, sixth and seventh will be treated in greater detail, and in addition to the description and comparison of the morphological features, I shall discuss their ecological relations and geographical distribution.

In this place I shall not review the work of others on the microscopic structure of the apically dehiscent anther or present the results of my own studies in this phase of the problem. I wish here to confine my attention to a discussion of the general morphological features and the ecologi-

cal relations of three groups, leaving the detailed treatment of these and the other types until a later time.

It seems hardly necessary to define here the terms dehiscence by apical pores, or apically dehiscent anthers. The terms have been used in the same sense as that in which they are regularly used by systematists. It may be proper to remark, that a precise definition offers considerable difficulty. Some genera have anthers opening by a single pore, sometimes at the tip of a rostrate prolongation of the anther, which is never increased down the sides by longitudinal slits; but, except for the Melastomataceae, in an equal or greater number of forms the pores are soon continued more or less down the sides in longitudinal slits. Between dehiscence by the most perfected terminal pore or pores and the primitive longitudinal dehiscence there is a complete series of gradations. In this paper I have followed quite closely the usage of the best systematists in the description of my material. If an anther shows well defined openings at the tip and there is reason for believing that the pollen is shed largely through these pores, it is generally designated in descriptive works and floras as apically dehiscent, or described: "anthers dehiscing by apical pores soon continued down the sides in longitudinal slits." Only living material would permit of an absolute determination. A large proportion of the anthers are thinner along the lateral furrows where dehiscence usually occurs in forms in which the anthers do open by lateral slits, and in herbarium material they are liable to be broken along this line even when such might not occur normally in the living plant. Sections cut from anthers which have not broken along this line are very apt to break apart at this point. It is far from easy or even quite impossible to determine whether the lateral slit is a natural occurrence or whether it is due to manipulation. These points will be considered for the forms examined in my final paper,



but for the present I have used the term in the rather general sense in which it is employed in descriptive botany.

In this paper I have omitted all reference to the literature. It is proper to state that I have examined all the most important systematic works treating of the forms here discussed as well as the special literature of floral ecology. These citations I hope to include with ample descriptions and illustrations of all of the forms considered, in the final paper.\* I have also sought to avoid all references to theoretical considerations and to confine myself as strictly as possible to the facts and the problem of grouping them in as logical and significant a manner as possible.

#### THE TYPES OF APICALLY DEHISCENT ANTHERS.

The classes recognized are the following: —

1. ARACEOUS TYPE.
2. GRAMINEOUS TYPE.
3. POLYGALACEOUS TYPE.
4. ERICACEOUS TYPE.
5. DILLENACEOUS TYPE.
6. SOLANUM-CASSIA TYPE.
7. MELASTOMATACEOUS TYPE.

The first four are to be merely touched upon in the present paper. The last three, on the other hand, are to be considered in some detail; they are characterized by many similarities of structure and doubtless of ecological relationship as well, and while, as it seems to me, they are separated, on the whole, by sharp mean differences, there is often difficulty in drawing the limits of the groups. Since they are to be understood only when examined com-

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\* Most of the titles to which reference has been made by the author's name only in this essay, may be found in the bibliographies in the English edition of Müller's *Fertilisation of Flowers*, the continuation of this list from 1883 to 1889 published by MacLeod in the *Botanisch Jaarboek*. 2: 195-254, 1890, or the more complete bibliography of Knuth's *Handbuch der Blütenbiologie*.

paratively, their essential points of difference may be stated.

The Ericaceous type as limited in this paper contains some forms which are closely related to those of the three following, but they will be left out of consideration here.

The Dilleniaceous, Solanum-Cassia and Melastomataceous types have in common a widely patent corolla, or at least a widely expanded corolla limb, and elongate, usually linear, basifixed anthers. The Dilleniaceous type differs from the other two in the possession of a larger number of stamens, with anthers inserted on generally long filaments, and often separate styles. The Solanum-Cassia type differs from the Dilleniaceous in the number of stamens, their much reduced filaments, and their frequent approximation around the style. The Melastomataceous type is characterized by anthers of the same general form as those of the Solanum-Cassia type, but it is sharply separated by the elongate and highly differentiated filament.

#### I. ARACEOUS TYPE.

Flowers usually densely crowded on a spadix; perianth generally much reduced; filaments usually shortened; anthers free or very often connate in a synandrium, bilocular or multilocellate, each locule dehiscing by a more or less irregular apical rent, or in a few cases, through a produced tubular process; pollen free or conglomerate in a vermiform column.

To this type belong many of the genera of the Araceae and Balanophoraceae. Other genera of these families shed their pollen through longitudinal slits in the usual way. The Loranthaceae and Lacistemaceae furnish interesting forms for comparison.

The geographical distribution and the floral ecology of this type will not be discussed here. It is clearly distinct from others to be treated later and to which I wish to direct especial attention.

## II. GRAMINEOUS TYPE.

In the characteristic anthers of the grasses the locules usually open by longitudinal slits extending from above downward, but more rarely (in some *Andropogoneae*) by a hole at the apex, often finally continued down the side in slits. This type likewise is clearly distinct from all others, and I shall not consider it further in this place.

## III. POLYGALACEOUS TYPE.

Flowers strongly zygomorphic, with highly differentiated perianth; androecium included in a ventral carina, usually monadelphous; anthers short, generally cupuliform, basifixed, dehiscing by a large, upper, terminal opening embracing both locules (*Polygalaceae*) or by two terminal pores (*Fissicalyx*).

This group contains the *Polygalaceae* and the single genus of the *Papilionatae* in which the anthers open by apical pores. In structure and geographical distribution, this is an interesting type, but cannot be treated in detail.

## IV. ERICACEOUS TYPE.

Under this type I have grouped with its special representatives a number of structurally very dissimilar forms. This has been done largely because of the systematic relationship of the material; it has been deemed best to treat all the *Ericaceae* together and in this paper I have placed with them a few other genera systematically related or similar in their floral structure. This type will not improbably be broken up later, but at the present time I do not care to treat in detail the various forms which I have here assigned to this type, and since they are, for the most part, quite distinct from those to which I intend devoting the body of this paper, they may be passed over with merely a general description.

Flowers hermaphrodite, regular or rarely zygomorphic;

corolla gamopetalous, globose, urceolate, tubular, infundibuliform, campanulate or almost rotate, generally 4–5-lobed, very rarely divided to the base; stamens usually twice as many as the lobes of the corolla, equal or alternately unequal, free or nearly free from the corolla, exserted or more generally included; filaments usually long, various in form; anthers basifixed or dorsifixed at the base or below the middle, rarely at the apex, dehiscing by large apical pores or more or less extensive slits, sometimes produced in one or two often very long terminal tubes opening at the top with small pores or more or less extensive slits, sometimes provided dorsally with aristae or setaceous appendages.

All Ericaceae are here included in this type. *Galanthus* and *Leucojum* of the Amaryllidaceae, with their pendulous flowers and perianth closely approximated around the androecium, may also be tentatively assigned to this type. *Pentaphylax*, the type of a family from China, may best be treated here, as may also *Clethra* of the Clethraceae, *Costaea* of the Cyrillaceae, and *Chimaphila* and *Pirola* of the Pirolaceae.

The floral ecology of this group is not discussed here. Our knowledge is chiefly of the Ericaceae and the two genera from the Amaryllidaceae. Many of the data bearing upon these will be found recorded in the Handbuch of Knuth.

#### V. DILLENIAEACEOUS TYPE.

Both whorls of perianth usually developed, but one or both sometimes reduced, usually campanulate or rotate in disposition; *stamens indefinite in number*; filaments long or short, free or variously united; *anthers mostly elongate, basifixed*; flowers usually actinomorphic throughout, but androecium sometimes zygomorphic, gynoecium of distinct or variously united carpels; flowers generally highly colored and conspicuous.

The sharp distinction of several of the members of this type from those of the following classes is quite impossible, but it seems helpful to make the division.

This class exhibits, with the possible exception of the Ericaceous type, the widest range of form and structure of any recognized. To it I have assigned four species of *Hibbertia*, *Acrotrema* *Schumacheria*, *Dillenia* and *Saurauia* of the Dilleniaceae, *Elaeocarpus*, *Sloanea*, *Vallea*, *Aristotelia* and *Dubouzetia* of the Elaeocarpaceae, *Ochna*, *Lophira* and *Cespedesia* of the Ochnaceae, *Tremanthera* of the Theaceae, *Bixa* of the Bixaceae, and *Plagiopteron* of the Flacourtiaceae.

#### Dilleniaceae.

The flowers of the Dilleniaceae are hermaphrodite, polygamous or dioecious, with usually five persistent sepals and as many deciduous petals which are patent during anthesis. The stamens are indefinite, usually numerous, and various in form, the gynoecium is usually composed of several more or less united carpels with free and for the most part widely divergent pistils with simple stigmas.

In *Hibbertia* (about 100 species, mostly confined to Australia) the dehiscence is said to be by pores in one section represented by 4 species, but I am not sufficiently acquainted with the forms. *Acrotrema* (about 12 species of India, Farther India and Ceylon) has many — 15–50 — stamens, free or more or less united into 3 or 4 bundles, and linear or sometimes ovate anthers generally opening by two apical pores. *Schumacheria* (with 3 species in Ceylon) is distinguished by zygomorphy. The linear or broadly linear anthers open, according to Gilg, at the top with two little holes which gradually increase more or less down the sides in longitudinal slits. *Dillenia* (of about 23 species distributed over tropical Asia, the Indo-Malay region, New Guinea, the Philippines, and Australia) has usually very long anthers which generally open at the top by two pores which may sometimes become confluent into

one or may be increased down the sides in longitudinal slits. The flowers are often very large and conspicuous; *Saurauia* (with about 98 species of tropical Asia and America, rare in Brazil and Guiana) has the anthers turned outward in the bud, but reversed and erect at the time of flowering, each of the two short, sometimes somewhat divergent locules opening by large pores or, more rarely, by longitudinal slits.

An indefinite number of stamens is characteristic of the Dilleniaceae, but in many forms a marked tendency to numerical reduction is observable, as is well seen in *Hibbertia*, but from the data available I am unable to draw any definite conclusions as to the relation between the number of elements in the androecium and the method of dehiscence. The forms of filament and anther are quite various. Apical dehiscence is confined almost exclusively to the elongate, basifixed anther. With the exception of one genus, the apically dehiscent forms all occur in the Dillenioideae with basifixed anthers and, in the exception, *Saurauia*, the versatile anthers are attached near one end and assume a more or less erect position at the time of flowering.

#### Elaeocarpaceae.

An important difference between the Elaeocarpaceae and the preceding family is found in the gynoecium. In the Elaeocarpaceae, the pistil is simple and filiform with only a possible indication of the compound nature of the ovary in the slightly lobed stigma of some forms.

*Elaeocarpus* (over 100 species of tropical Africa, Asia, Australia, the Pacific Islands, New Caledonia and New Zealand), *Sloanea* (50 species in the tropics of both hemispheres), *Vallea* (3 species in the mountains of New Granada and Peru) and *Aristotelia* (7 species, 3 in Australia, 3 in New Zealand, 1 in Chile) have campanulate or more or less patent, often highly colored and fringed perianth segments; stamens indefinite in number; anthers linear, basi-

fixed, obtuse or provided with a terminal appendage, dehiscing by 1 or 2 apical pores, sometimes continued down the side in slits.

In *Crinodendron* (2 species in Chile) and *Antholoma* (2 species in New Caledonia) the corolla is urceolate and the anthers open by longitudinal slits, which may open more widely above or originate in a poriform opening, or may be confined to the upper portion of the anther. *Dubouzetia* (represented by 1 or perhaps more species in New Caledonia) has in some ways a very similar floral structure, but the dehiscence is by a single bilabiate terminal pore.

The Elaeocarpaceae is a highly interesting group and I am far from satisfied with the treatment which can be given it in this paper.

#### Ochnaceae.

All genera of the Ochnaceae are to be considered in a paper on apically dehiscent anthers. The flowers show a considerable diversity of form and are to be referred to different types.

*Ochna* (about 25–30 species distributed over tropical Asia and Africa, only a few species — 3, *fide* Flora Capensis — in the Cape region) has numerous stamens with long, filiform filaments and oblong or linear, basifixed anthers dehiscing by apical pores or longitudinal slits. It belongs clearly to the Dilleniaceous type. *Lophira* (1 species in central and west Africa) with the linear anthers dehiscing by short, terminal, almost poriform slits, belongs here, as does also *Cespedesia* (3–4 species in Peru, New Granada and Panama) with 40–60 elongate, linear, curved anthers on short filaments, all turned toward the same side of the flower during anthesis.

*Elvasia* and *Godoya* may be mentioned here as forms in which the stamens are more numerous than is common in the *Solanum-Cassia* type, but for other structural reasons, these, as well as the other members of this family, will be considered with the members of that group.

## Theaceae.

With *Tremanthera* (1 species in New Guinea), the single apically dehiscent genus of the Theaceae, I am not sufficiently acquainted, but the indefinite number of stamens with long-ovate anthers would indicate that it should be placed in this class.

## Bixaceae.

In the Bixaceae, *Bixa* (1 species of tropical America, now widely distributed in the tropics) is a unique form characterized by its numerous, horse-shoe shaped anthers on long filaments. It may most conveniently be placed in this type. The other two apically dehiscent genera will be treated under the Melastomataceous type.

## VI. SOLANUM-CASSIA TYPE.

Perianth usually quite large, mostly actinomorphic, segments campanulate or *more generally patent or reflexed* in disposition; androecium of few members, usually 5 or 10, very rarely as many as 15, staminodia sometimes present as reduced members of these numbers in zygomorphic forms or more rarely from a multi-staminate androecium; filaments *much reduced in length*; anthers basifixed, oblong to sagittate or linear, often more or less connivent around the filiform style with its small, generally simple stigma, or at least erect, very rarely distant; flowers generally conspicuous and highly colored.

This is the type upon which my interest has been for the most part centered. It shows a great uniformity of character and in this lie its especial interest and importance as a source of data towards the solution of the problem of the influence of insects upon the form of flowers and the geographical distribution of different floral types. In view of this fact, the treatment of this class is more detailed than that of the others.

As I have insisted above, the distinction between dehiscence by pores and by longitudinal slits, and between the



*Solanum-Cassia* type and any other is not an absolute one. The number of apically dehiscent genera or species might be easily increased or decreased by including forms in which the lateral slits first open more widely at the tip, or including all those in which the pores are finally supplemented by lateral slits at length continued more or less down the side. The number of genera as I have limited it is, I feel confident, approximately right so far as may be determined from systematic literature and the examination of herbarium material.

To the *Solanum-Cassia* type I have assigned 59 genera. Of these, 19 are Monocotyledons and 40 Dicotyledons. The Monocotyledons are: *Mayaca* (Mayacaceae), *Schoenoccephalum*, *Stegolepis*, *Rapatea*, *Saxo-Fridericia*, *Cephalostemon*, *Spathanthus* (Rapateaceae), *Cartonema*, *Dichorisantha* (Commelinaceae), *Monochoria* (Pontederiaceae), *Walleria*, *Agrostocrinum*, *Dianella*, *Calectasia*, *Luzuriaga* (Liliaceae), *Conanthera*, *Cyanella*, *Zephyra*, *Tecophilaea* (Amaryllidaceae). The Dicotyledons are: *Cheiranthra* (Pittosporaceae), *Cassia*, *Koompassia*, *Distemonanthus*, *Labichea*, *Dicorynia*, *Baudouinia*, *Duparquetia*, *Krameria*, *Martiusia* (Leguminosae), *Platytheca*, *Tetratheca*, *Tremandra* (Tremandraceae), *Thomasia*, *Guichenotia*, *Lysiosepalum*, *Lasiopetalum* (Sterculiaceae), *Ouretea*, *Brackenridgea*, *Godoya*, *Elvasia*, *Blastemanthus*, *Wallacea*, *Schuurmansia*, *Poecilandra*, *Luxembergia*, *Euthemis*, *Leitgebia* (Ochnaceae), *Stemonoporus*, *Monoporandra* (Dipterocarpaceae), *Kiggelaria* (Flacourtiaceae), *Begonia*, sections *Solanthera* and *Parvibegonia* (Begoniaceae), *Ardisia*, sections *Icacorea*, *Stylogyne*, and *Monoporus* (Myrsinaceae), *Gardneria* (Loganiaceae), *Exacum*, *Cotylanthera* (Gentianaceae), *Solanum*, *Cyphomandra* (Solanaceae), *Argostemma*, and *Strumpfia* (Rubiaceae).

#### Mayacaceae.

In the Mayacaceae, with the single genus *Mayaca*, we

have a very good representative of this type, although the anthers offer some peculiarities of structure. (Ten species; all but one, which is found in Lower Guinea, are American; 1 very similar to and possibly identical with a South American form occurs in eastern North America, 1 occurs in Cuba, and the others in Brazil, Peru and Guiana. Brazil has six species.)

#### Rapateaceae.

The Rapateaceae is a family of six genera and about 19 species in tropical South America. Its position in this group is somewhat questionable on account of the moderately long perianth tube formed by the lower portion of the segments. The limb, however, is patent, the anthers basifixed and linear and shedding their pollen through terminal pores or a single terminal pore, sometimes provided with a terminal, spoon-like prolongation of the tip of the anther.

#### Commelinaceae.

The Commelinaceae is represented by two genera besides the highly interesting *Cochliostema* to be described later. *Cartonema* (5 or 6 species confined to tropical Australia) shows a considerable range of form in the structure of the anther. In some species, dehiscence is by longitudinal slits; dehiscence by pores seems to be in a less perfected state than in the tropical American *Dichorisandra* (about 27 species, almost exclusively Brazilian). This genus is a highly interesting and very characteristic representative of the Solanum-Cassia type.

Except for minor differences, a considerable degree of uniformity prevails in the floral structure of the Commelinaceae. The petals are patent, except in about 3 genera in which they are unguiculate and united into a usually narrow tube, and 1 in which the perianth is tubular below, but even here the limb is generally patent. The basifixed anthers show a wide range of form, while the

filaments may be naked or provided with hairs. Thus, excepting the character of dehiscence, with perhaps a slight elongation of the anthers, the flowers of the two forms treated here do not differ widely from the other genera of the family. In floral structure, the most highly organized member is *Cochliostema*, to be discussed later.

#### Pontederiaceae.

*Monochoria* (3 species, 1 in tropical East Asia, 1 in tropical and subtropical Asia and East Africa, and 1 in Australia), of the Pontederiaceae, has the corolla and the form of the anthers of this type. The filaments are not so reduced in length as is generally the case, and the terminal pores are soon continued down the sides in longitudinal slits.

A comparison of the disposition and form of the stamens in their relation to the length and form of the perianth tube in the other genera of this family is interesting. In *Heteranthera* the perianth tube may be very long and narrow, but the limb is widely patent. In the other genera, the perianth is more widely expanded from the base but still shows a tube of considerable length. Only in *Monochoria* is the tube wanting and the elements of the perianth, which are almost free to the base, widely patent. Concerning the form of the stamens it may be said that in *Eichornia*, *Pontederia* and *Reussia*, the markedly zygomorphic androecium is characterized by filaments of considerable length with basifixed or nearly basifixed and short, thick anthers which may be included or widely exerted, In *Heteranthera* the anthers are sometimes more elongate, approaching linear in form. The filaments, inserted at the top of the corolla tube, may be of the same length as the anthers or much longer. In *Monochoria*, the filiform filaments are of about the same length as the anthers, which seem to be the most elongate in the family, and, perhaps, with walls of firmer texture.

## Liliaceae.

Of the Liliaceae, five genera may be mentioned: *Walleria* (three species, or perhaps only three varieties of the same species, in tropical Africa, with 1 extending into South Africa, and another from Madagascar) is one of the finest illustrations of this type which I have seen. *Agrostocrinum* (1 Australian species) is another good representative with somewhat zygomorphic flowers. *Dianella* (11 species, 1 widely distributed in the Mascarene Islands, tropical Asia, Australia, New Caledonia and the Sandwich Islands, 8 more in Australia, 1 in New Zealand, Norfolk and Fiji and Society Islands and 1 in the Isle of Pines and New Caledonia), with variously thickened filaments and anthers in which the pores are sometimes continued downward in introrse longitudinal slits, also belongs here. The flowers of *Calectasis* (1 West Australian species) are among the most beautiful of those assigned to this type. *Luzuriaga* is a highly interesting genus of South Pacific or antarctic distribution. Four species are described. In three species (of which 1 is confined to New Zealand, 1 occurs in Patagonia, Tierra del Fuego, Falkland Islands and New Zealand, and 1 is found only in Chile and Peru) the flowers have a very close similarity to other members of the Solanum-Cassia type, but dehiscence seems to be by longitudinal slits, although it has been described as by pores and it may be so at first, as in *Monochoria* and various other forms. The fourth species (reported only from South Chile) has a different floral structure. The anthers are borne on longer filaments and at the time of flowering are reflexed and open, at least at first, by two basal pores. The reflexed stamens are quite closely approximated around the ovary so that the general habit of the flower agrees very closely with that of many other forms in this class.

*Odontostomum* is an aberrant form from California which will be considered later.

## Amaryllidaceae.

Pax in his treatment of the Amaryllidaceae in *Die Natürlichen Pflanzenfamilien*, characterizes two tribes, Galanthinae and Conanthereae, as dehiscent by apical pores. The genera of the Galanthinae have been mentioned under the Ericaceae type.

*Conanthera* (3 or 4 species in Chile) has the anthers connivent in a cone and dehiscent by pores at the tip or by introrse slits extending almost to the base. They are provided at the tip with a simple or bifid acumen and are either exerted or included in the campanulate perianth tube. *Cyanella* (4 or 5 species in the Cape region) is a beautiful example of this type with some species showing zygomorphic flowers, in some respects very similar to those of *Cassia*. *Zephyra* (1 species in Chile) and *Tecophilaea* (2 species in Chile) are aberrant, zygomorphic forms which cannot be described in detail here.

A point of interest in the relation of the apically dehiscent genera of the Liliaceae and Amaryllidaceae to the other members of the families is that in the arrangement of Engler and Prantl the apically dehiscent genera of the former are found associated with sometimes several of the longitudinally dehiscent forms in as many of the ultimate groups as there are genera, belonging to three of the subfamilies of that system, while in the Amaryllidaceae, the four genera assigned to the Solanum-Cassia type all belong to the same ultimate group.

A comparison of these groups in the two families is interesting. In the Amaryllidaceae the four apically dehiscent genera belong to a single group and are structurally very similar, differing largely in the characteristics of the variously zygomorphic androecium. In the Liliaceae, however, the differences to be noted within the same group are much greater, as may be most strikingly illustrated by the comparison of *Walleria* with *Gloriosa*

*Sandersonia*, and *Tricyrtis*, while other members of the group also show considerable differences in structure, and none of them at all closely approach the form of the apically dehiscent genus. In the twenty genera of the Anthericinae, the group to which *Agrostocrinum* belongs, however, the floral habit is quite uniform. In all, the corolla is rotate; in several, the filaments are long and the anthers short, but in others the filaments are much reduced in length and the anthers oblong to linear and sometimes tending to be more connivent around the style.

Space will not permit a detailed discussion of the floral structure of the two families. The two illustrations just given from the Liliaceae are perhaps representative. I think it may be said for these families that in the Amaryllidaceae the prevalent habit of the perianth is, roughly speaking, infundibuliform while in the Liliaceae it is patent or campanulate. In the Amaryllidaceae the four apically dehiscent genera stand almost alone as representatives of this floral habit while in the Liliaceae there are many genera with patent or broadly campanulate perianth. In the most of these genera the filaments are filiform, more or less elongate, and bear short, usually versatile anthers, but in several the filament is reduced in length while the anther is of the more elongate form commonly seen in the apically dehiscent genera. The forms which in their general structure bear a close resemblance to the apically dehiscent *Solanum-Cassia* type are almost wanting in the Amaryllidaceae. It must not be understood that they are identical with the apically dehiscent genera except for the difference in the method of the opening of the anthers. I do not go so far as to state that they represent incipient stages of members of this class, for in the interpretation of such facts as these, the greatest caution must be exercised. It must be pointed out, however, that in the general habit of the flower there is not the sharp line of distinction be-

tween apically and longitudinally dehiscent forms in the Liliaceae that there is in some other families.

We may now pass to the Dicotyledons.

#### Pittosporaceae.

We find in *Sollya* (2 Australian species) of the Pittosporaceae a form similar in structure to the section *Lycopersicum* of *Solanum*, but not showing dehiscence by pores, and *Cheiranthra* (4 Australian species) which is an excellent, slightly zygomorphic representative of this type.

In the Pittosporaceae the five petals, frequently more or less unguiculate, are erect and connivent or coherent in a tube at the base and spreading above. In only a few species besides those of the genera *Sollya* and *Cheiranthra* are the petals more or less patent from near the base. Another most important difference between these two genera and the others of the family is the relative size and proportion of the parts of the stamen. The anthers are longer than the filaments in *Sollya* and *Cheiranthra*, while in the other genera they are shorter than the filaments, and, in relation to other parts of the flower, smaller than in the genera considered here. These two genera are aberrant forms in the family.

#### Leguminosae.

In the Leguminosae the apically dehiscent genera are, with one exception, confined to the Caesalpinioideae, and in this sub-family, with one exception, to the Cassieae.

*Cassia*, serving as one of the types of this group, is too well known to require description. (About 412 species of tropical and subtropical distribution are known, extending in America from Patagonia into the United States and reaching their highest differentiation in the tropics of the New World — 290 species. Australia has about 33 species, tropical Africa 27, the Indian, Malayan and Oceanic Island region about 34, and the Cape region 5 or 6).

In *Koompassia* (represented by 2 or 3 species, gigantic

trees, confined to Malacca and the Malay Archipelago) the stamens of the species differ considerably in form, those of one species being much broader than those of the other, and possibly in dehiscence.

*Distemonanthus* (1 species found in Upper Guinea) is a strongly zygomorphic form with only two fertile stamens, clearly belonging here.

*Labichea* (5 Australian species) is very closely related to *Cassia* and with almost identical floral structure except that the stamens are reduced to two.

*Storckiiella* has the perianth quite widely patent and the linear anthers of this type, but the elongate filaments make it necessary to place it in the Melastomataceous type.

*Dicorynia* (4 species in Guiana and North Brazil), with its two short, thick anthers, one of which is sometimes eight-locellate at the tip, is a unique form, but one which seems best treated here.

*Baudouinia* (2 species in Madagascar) has linear-sagittate, basifixed, apically acuminate and penicillate anthers, both locules of which open at first by an introrse subapical fissure which soon extends in two introrse longitudinal slits to the base.

In *Duparquetia* (a single species, a richly flowering shrub, in west tropical Africa) the flowers are, with the possible exception of *Krameria*, the most strongly zygomorphic in this type. The four anthers dehisce by short, terminal slits which are not continued down the side for more than a third of the whole length of the anther.

*Martinsia* (2 species in Brazil and British Guiana) is one of the largest-flowered and most typical, slightly zygomorphic, representatives of this type.

*Krameria* (23 species, distributed from warmer North America to Chile), of somewhat uncertain systematic affinities, is now placed next to the Cassieae in the Leguminosae. Structurally it is the most aberrant form assigned



to this type, but it may be treated here, provisionally, at least.

In the Leguminosae, the apically dehiscent forms of this type are confined, with the single exception of *Krameria*, to the Cassieae of the Caesalpinoideae. The genera of the Cassieae are distinguished from all others of this subfamily except *Krameria* by their usually basifixed, apically dehiscent anthers, those of all other genera being dorsifixed and versatile and with longitudinal dehiscence. In examining the genera of the Cassieae itself I find that the apically dehiscent forms have, as compared with the others, a more elongate anther and a shorter filament. The patent corolla is general in the Caesalpinoideae but the form of the anthers in the apically dehiscent genera will, I think, be found quite different from that of the other genera.

#### Tremandraceae.

The Tremandraceae (represented by 3 genera of about 23 species endemic in West and South Australia) constitute the only dicotyledonous family in which all the species are apically dehiscent. The four parallel cells in the same plane in the anthers of *Platytheca*, and the terminal tube opening by a single pore in this genus and *Tetratheca* merit especial mention. The genera of this family, while offering some minor points of difference from the others, must be regarded as among the most highly specialized of this type.

#### Sterculiaceae.

In the Sterculiaceae, *Hermannia* shows dehiscence by longitudinal slits, but the habit of the androecium is so similar to that of *Solanum*, *Borago* and some other forms that it may be mentioned for comparison.

In *Thomasia* (21 species, all but 1 confined to Australia) much the same condition prevails except that here the ovate or oblong anthers, connivent in a cone around the ovary, dehisce by short, sometimes almost poriform, introrse

slits, finally extending more or less down the sides. The pistil sometimes considerably exceeds the tips of the stamens.

*Guichenotia* (5 species endemic in West Australia) has anthers opening by introrse terminal pores or slits which may be continued down the side.

*Lysiosepalum* (2 species are found in West Australia) has the anthers subulate to linear and dehiscing by apical poriform slits which may be finally continued down the sides.

*Lasiopetalum* (25 Australian species, mostly confined to West Australia) is probably the best representative of the *Solanum-Cassia* type to be found in the Sterculiaceae. Even here the pores of the anthers are continued down the sides and the style is sometimes much exerted and covered with stellate hairs.

It is unnecessary to discuss in detail here the polymorphic and often complicated floral organization in the Sterculiaceae. The forms showing dehiscence by pores or short slits are found only in the *Lasiopetaleae*, which differs very essentially from the other tribes in its floral structure. All members of this group agree in the possession of a patent perianth. The petaloid nature of the sepals and the reduction of the petals to scale-like structures, the peculiar style in some species and the floral habit of other genera of the family to which these forms have been assigned give them a peculiar interest, but our knowledge of them is entirely too meager to permit of any suggestions as to the significance of the forms.

#### Ochnaceae.

In the Ochnaceae, we have a family particularly difficult of treatment on account of the numerical reduction in the androecium. Transitions are present between the *Dilleniaceae* and the *Solanum-Cassia* type, while some of the

forms are strongly suggestive of the Melastomataceous type.

*Ouratea* (76 species in tropical America and 26 in the Old World) is one of the finest examples of the Solanum-Cassia type, sometimes with more or less rugose anthers. *Brackenridgea* (5 species, 2 in the Fiji Islands, 1 in Penang, 1 in Queensland, 1 in Zanzibar) is an excellent representative of the floral habit of this type, but the anthers open by longitudinal slits or at first by apical pores which are later increased more or less towards the base in longitudinal slits. *Godoya* (3 species in Peru and New Granada) has 10 to 20 stamens but their form is such that they seem to be more properly treated here than in the Dilleniaceous type. *Elvasia* (4 species in Brazil and Guiana) with stamens 8 or indefinite, up to 20, with oblong or nearly oval anthers basifixed on more or less elongate, filiform filaments, suggests in some of its species the Melastomataceous type, but in others the filaments are reduced in length and the anthers more elongate, so it may be treated here.

*Blastemanthus* (2 species from the upper Amazon, of which 1 also occurs in Guiana) has the 10 declinate stamens with very long anthers on short filaments surrounded by numerous staminodia. As far as form is concerned, *Wallacea* (1 species in the upper Amazon region) is an excellent representative of this type. The fertile stamens are 5 in number and turned to one side at the time of flowering. Staminodia are present, and the terminal pores, or single terminal pore, of the anthers are said to be later continued down the sides in lateral slits. In *Schuermansia* (3-4 species in the Indian Archipelago) the floral structure seems to be very similar to the preceding. *Poecilandra* (1 species in northern Brazil and British Guiana) may be placed without question in this type. *Luxemburgia* (7 species, all in Brazil) is a peculiar genus in which the indefinite, usually few, anthers are aggregate or connate in a column on one side of the ovary. *Euthemis* (3-4

species in the Indo-Malay Archipelago) is a good example of this type.

The numerical reduction in the androecium of the Ochnaceae may be mentioned in this connection. The family is characterized by elongate, basifixed anthers, generally dehiscing by apical pores, with some species of several of the genera showing, at least finally, longitudinal slits. I have been unable to convince myself of any unquestionable relation existing between the stage of reduction in the number of stamens and the perfection of dehiscence by pores in this family except in the following special cases. While too much weight must not be attached to the limited evidence, the condition of stamens and staminodia in certain genera may be described.

In *Neckia* (3 species in the Indo-Malay Archipelago) the staminodia of the inner whorl, about 10 in number, are clavate and cohere with the filaments of the longitudinally dehiscent anthers at the base. In *Leitgebia* (1 species in the savannahs of Brazil) a similar condition occurs with only 1 whorl of 5 spatulate staminodia and anthers dehiscing at first by apical pores. In *Sauvagesia* (11 species, confined, with the exception of 1 of universal tropical distribution, to tropical Brazil) two whorls are present, the outer of filiform staminodia, the inner of 5 petaloid structures, closely approximated in a cylinder around the longitudinally dehiscent anthers. In *Lavradia* (6 species endemic in Brazil) is to be seen a still more modified condition. The outer whorl of staminodia is entirely wanting while the members of the petaloid whorl are connate in a coniform or almost urceolate corona surrounding the shortened anthers which seem to show no trace of apical pores, but open longitudinally from the first. These aberrant forms may be profitably compared with *Antholoma* of the Elaeocarpaceae. While the evidence is far from comprehensive, it

strongly suggests the significance of the exerted condition of the anthers in apical dehiscence.

#### Dipterocarpaceae.

In the Dipterocarpaceae, species of *Shorea*, *Anisoptera* and *Vatica* have anthers opening more or less terminally, but the only genera to be considered in this paper are *Stemonoporus* (12-13 species endemic in Ceylon), and *Monoporandra* (2 species endemic in Ceylon), both of which in the general habit of the flower fall clearly into the *Solanum-Cassia* type.

#### Flacourtiaceae.

Of the Flacourtiaceae, *Kiggelaria* (3 South African species) may be assigned to this type.

#### Begoniaceae.

In the Begoniaceae, *Begonia* is the principal genus, being represented by about 400 species throughout the warmer regions of the whole world. In all the species, the stamens are numerous, anthers basifixed, rarely almost spherical, usually ovate or oblong to linear, connective produced in various forms beyond the locules or not, filaments long or short as compared with the anthers, free or monadelphous. The dehiscence is by lateral slits. In two Brazilian species, forming the section *Solanthera*, the filaments are free, anthers linear, obtuse, much longer than the filaments and opening at the apex through two pores. In the section *Parvibegonia*, of 8 Indian species, dehiscence is said to be lateral, by short, subapical slits in six species, and by "pores" in the other two. My knowledge of the Indian species is very incomplete, but the Brazilian forms may certainly be placed in this type.

#### Myrsinaceae.

In the Myrsinaceae, *Cybianthus*, with small broad anthers dehiscing by elongate or short and subapical, some-

times almost poriform slits, is an interesting form but hardly merits consideration as one in which dehiscence is by apical pores.

*Ardisia* is a large genus of over 200 species much in need of revision. The stamens are 5 in number, with short sagittate or lanceolate anthers usually opening by longitudinal slits. In the section *Icacorea*, however, according to Pax, the anthers open by apical pores. This section seems to comprise about 7 South American species. The anthers of the second section, *Stylogyne*, with 1 Brazilian and 1 Malayan species, are described as opening by terminal pores. In the single representative of the third section, *A. paludosa* of Madagascar, the anthers open by a single terminal pore. In the two other sections of the genus containing the remainder of the species, distributed throughout the tropics of both hemispheres, dehiscence is by lateral slits. My knowledge of this genus is very imperfect, but I think it probable that an examination of suitable material would show that in the most of the above species described as apically dehiscent the pores are not permanent, but merely the beginnings of longitudinal slits.

#### Loganiaceae.

In the 32 genera assigned to the Loganiaceae only 5 or 6 have any species with a rotate corolla, the tendency being towards tubular, salver-form or campanulate. *Gardneria* is the only genus characterized by a rotate corolla with oblong to linear exserted anthers. Three species are found in Japan and India. In *G. nutans* (of Japan) the slits are said not to extend to the base as in the others, but to be confined to the tip of the anther.

#### Gentianaceae.

In the Gentianaceae, two genera belong clearly to this type: *Exacum* (29 species, distributed over tropical and sub-tropical Asia, the Malay Archipelago, Madagascar and

tropical Africa, with 4 species in tropical America), and *Cotylanthera* (3 species, saprophytic herbs, from Java, Mariana Islands and the Himalayas). *Chironia* and *Deianira* are interesting for comparison, though they can hardly be included in the list.

In the Gentianaceae the corolla is infundibuliform, hypocrateriform, campanulate or sometimes rotate. In both *Exacum* and *Cotylanthera* the corolla has a short, subglobose tube with patent limb and stamens inserted in the throat. A detailed comparison of the floral habit of these genera with the other members of the family is precluded by lack of space. Several genera approach the rotate corolla characteristic of the *Solanum*-*Cassia* type either by way of a broadly campanulate corolla or by a hypocrateriform corolla with a usually shortened cylindrical tube and prominent patent limb. In some of these forms the stamens are included while in others they are exserted, but with short, versatile anthers on longer filaments. In some cases the anthers are linear but versatile, while in others they are linear and basifixed. A few forms approach very closely in their floral habit the two apically dehiscent genera.

#### Solanaceae.

In the Solanaceae, two forms are to be considered, *Solanum* and *Cyphomandra*. *Solanum* (of about 970 nominal species 630 occur in Tropical America, 70 in extra-tropical South America, 27 in tropical Africa, 10 in the East African islands, 34 in the Indian, Malay and Oceanic Island region, 26 in South Africa and 52 in Australia) is too well known to require description: attention may be directed to the few zygomorphic forms constituting the section *Nycterium*, and to the considerable number of species showing incipient stages of this characteristic, and to the condition prevailing in the small section *Lycopersicum*. In many of the species the pores are later continued down the sides of the anthers, sometimes to the base, in

longitudinal slits. *Solanum* furnishes one of the classic illustrations of the apically dehiscent anther, and the large number of species in which the pores are continued down the sides in longitudinal slits stands as a justification for including in the apically dehiscent category several genera in which the pores are later supplemented by lateral slits. Between the two forms of dehiscence, no sharp line exists although in the individual cases it is usually not difficult to decide very satisfactorily to which category a form should be referred.

In *Cyphomandra* (about 35 tropical American species, especially numerous in Brazil, and 2 extratropical South American species), the species of which were formerly treated under *Solanum*, the structure of the anther differs somewhat from that of *Solanum*. In some of the species at least, the walls are very thin and elastic, so that the pollen is puffed out by a bellows-like action. This genus is, in my present judgment, to be regarded as a specialized representative of the *Solanum*-*Cassia* type.

In the Solanaceae the gamopetalous corolla is tubular, infundibuliform, hypocrateriform, campanulate or rotate. I shall not give here a detailed discussion of the structure or distribution of the genera or species which approach *Solanum* in floral habit, but from quite careful comparison I may state with some confidence that *Solanum* represents the form in which the anthers have attained the greatest length and the filaments are the most reduced.

#### Rubiaceae.

In *Argostemma* (30-40 species in tropical East Asia, 1 in West Africa), of the Rubiaceae, we have an interesting genus, some species of which belong clearly to this type. Only a few of the 30-40 species show dehiscence by pores, and I have not data which enable me to state which or how many these species are.

*Neurocalyx* (about 6 species especially in Ceylon, but



also extending to the island of Borneo and oriental Asia) is an interesting form for comparison, in which the anthers are connate in a cylindrical tube and open internally. The monotypic *Strumpfia*, of the rocky coast of the Antilles, is another form which may be profitably compared. The five anthers form a conical synandrium around the pistil. The locules open in a more or less irregular manner at the tip, the outer wall of the synandrium extending considerably above the inner one. To attempt a statement of the condition of the corolla, androecium, and gynoecium in the genera of this family, even were data for such a statement available, demands an unprofitable amount of space and time. A quite careful examination of the genera, however, has shown that in the most of those with a rotate or almost rotate corolla, the androecium is characterized by elongate filaments and short anthers. In some cases the anthers may be elongate or linear, but in these cases they are usually dorsifixed, sometimes near the base, and distant instead of connivent around the style. With the exception of *Argostemma*, *Neurocalyx* and *Strumpfia*, I have found no genera which I could confidently refer to the floral habit exemplified by *Solanum* or *Cassia*. All of these forms may be profitably compared with the section *Lycopersicum* of *Solanum* or with *Sollya* of the Pittosporaceae.

#### VII. MELASTOMATACEOUS TYPE.

This type is practically coextensive with the Melastomataceae, which furnishes almost all of its members. Possibly some of the genera from this family should be included under the *Solanum*-*Cassia* type on purely structural grounds, but considering the nature of the characteristics separating the two groups, it has been thought best to retain all such forms here.

The essential distinguishing characteristic of this type is, in my opinion, the elongated filaments. There is the same conspicuous, patent perianth as in the *Solanum*-*Cassia* type

with little indication of a special receptacle for nectar. The number of stamens is usually small. The anthers are basifixed and have generally the same elongate, linear or subulate, form as in the preceding type. The pores are often minute, both locules usually opening through a single pore, and are very rarely continued down the sides. Often the anther has thin, flexible walls which make possible a bellows-like action in the ejection of the pollen.

In the Melastomataceae, considering the size of the family, the floral structure is quite uniform. Flowers usually 4- or 5-merous; petals usually large and highly colored, never absent though sometimes reduced, rarely connivent into a tubular or campanulate corolla; stamens usually twice as many as petals, rarely as many, or in some cases indefinite, all similar or alternately reduced or imperfect; filaments long or short, thick or slender, straight or arcuate, glabrous or glandular; anthers basifixed, almost spherical or cuneiform to linear or subulate, the oblong to linear or subulate being the prevalent type, straight or variously curved, dehiscing by a single terminal pore, rarely by two terminal pores and very rarely by lateral slits or by four terminal pores. The connective shows many modifications and is often produced below the locules and variously appendaged. Style filiform, straight or curved; stigma usually minute, rarely capitate.

It seems unnecessary to enumerate or describe the genera. The more essential structural points and the geographical distribution of the forms may be obtained from the work of Bentham and Hooker or Engler and Prantl, the splendid elaboration of the South American forms in *Flora Brasiliensis* or the detailed monograph of the family by Cogniaux. An examination of the individual genera reveals the fact that there prevails in this family a marked structural uniformity which instead of being obscured by numerous minor differences, is only made more conspicuous by them. The family includes

161 genera of tropical and subtropical distribution, 98 occurring in South America, 31 in the Indian region, 19 in the tropical African region and the others of various distribution.

Outside of this family I have assigned only three genera to this type: *Storckiella* of the Leguminosae, and *Maximiliana* and *Amoreuxia* of the Bixaceae. Possibly some others, as, for instance, *Cheiranthera* of the Pittosporaceae and *Exacum* of the Gentianaceae should also have been placed here instead of in the Solanum-Cassia type.

*Storckiella* (2 species in Oceanica) is the only member of the apically dehiscent Cassieae not clearly belonging in the Solanum-Cassia type. It is the only form with long filaments and it seems best for this reason to separate it from the genera to which it is systematically related.

In the Bixaceae, *Bixa* has been treated under the Dilleniaceae type. *Maximiliana* (13 species, 6 in tropical America, 3 in Africa, 1 in tropical Africa and southern Asia, 3 in North Australia and Queensland) with large actinomorphic flowers, and *Amoreuxia* (3 species in Central America) with zygomorphic flowers, have long filaments and rather elongate anthers which open by well-formed terminal pores. These forms should possibly have been placed in the Dilleniaceae type too, but the form of the stamens is very suggestive of the Melastomataceae type so they have been placed here.

#### ABERRANT FORMS.

As mentioned above, a few genera in which the anthers have been described as opening by pores do not fall readily into any of the above types. The fact that the most of the forms described as apically dehiscent belong clearly to one of these categories has led me to designate these simply as aberrant forms. Here as elsewhere classification should not be too much influenced by the number of individuals or named groups of individuals which may be assigned to any

particular subdivision, but in our almost total ignorance of their ecology and in some cases of their structure it seems best to treat these forms in this way.

These so-called aberrant forms are the following:—

*Odontostomum* (1 species in California) of the Liliaceae has a hypocrateriform corolla with patent or reflexed lobes with erect, basifixed, ovoid anthers which are only about one-half or one-third as long as the filaments.

In the Euphorbiaceae, *Poranthera* (5 Australian species, of which one also occurs in Tasmania and New Zealand, and a sixth endemic in New Zealand) has small flowers with five stamens having 4-locellate anthers opening in four terminal pores which are quite distinct or sometimes confluent into two.

In the Ebenaceae, the anthers of the three species of the section *Leucoxylum* (2 in Madagascar and 1 in the Indian monsoon region) of *Diospyros* (about 120 species of wide distribution, especially numerous in the Indian region) are described as opening by lateral pores at the tip instead of by longitudinal slits as in the other species. The corolla in *Diospyros* is urceolate, campanulate, tubular, or salverform; stamens 4 to indefinite, usually 16; anthers oblong, linear or lanceolate. In the three species which have been described as apically dehiscent the flowers are small, the corolla seems to be openly campanulate and the stamens 10–16 in number. It may be that these species might be properly assigned to the *Solanum-Cassia* type. Sargent describes the sixteen anthers of *D. Texana* included in the urceolate corolla as dehiscing only near the apex and his figure represents the openings as almost poriform.

The condition prevailing in the Acanthaceae is one of particular interest. Here we have 7 genera which are said to have, in some species at least, anthers opening by apical pores. Of these, *Staurogyne* need not be considered, since dehiscence in this genus can hardly be justly described as by apical pores. *Ophiorrhiziphyllon* (1 species in Marta-

ban) is insufficiently known to me. The anthers of *Afromendoncia* (3 species in tropical Africa) are peculiar among those opening by apical pores. In *Hiernia* (1 species in Angola), *Mendoncia* (about 20 species in tropical America), *Monachochlamys* (1 species in Madagascar) and *Pseudocalyx* (1 species in Madagascar and Nossi Be Island) the anthers are of the simple oblong to linear type with the more or less shortened filament so characteristic of the apically dehiscent anthers of most of the preceding families. Except in one or two of these six forms, however, dehiscence is not by the clearly-defined, round pores found in so many of the genera described above, but by more or less elongate apical slits.

It is not necessary in this place to enter into a detailed discussion of the structure of the stamens in the usually strongly zygomorphic flowers of the Acanthaceae, but attention may be called to the fact that the form of stamens found in the four genera just mentioned is not at all common, in fact is almost unique, in this large family. In almost all the forms discussed above, the linear anthers on short filaments are exserted from a widely open corolla. In the Acanthaceae the corolla is rarely open enough to be designated as campanulate from the base and it is never rotate. In *Hiernia* the limb is patent and the somewhat declinate linear anthers exserted so that except for the considerable length of the tube the habit of the flower is much the same as if the anthers were inserted by short filaments on a rotate corolla. The presence of the long perianth tube alone prevents the placing of this interesting genus in the Solanum-Cassia type. In *Ophiorrhiziphyllon* the two fertile stamens with long filaments and short anthers are described as much exserted from the zygomorphic corolla. *Afromendoncia* has the tube somewhat expanded above and the characteristic anthers project only slightly. In *Monachochlamys* the corolla is tubular to campanulate, with the stamens clearly included, while in the two other

genera, *Mendoncia* and *Pseudocalyx*, the same condition prevails with a less widely open corolla tube and more elongate anthers. Data are too limited to justify speculation, but the association of a tubular corolla with apically dehiscent anthers of the form so generally found when the corolla is patent, is interesting. The inclusion of a linear anther in a cylindrical corolla tube is nothing out of the ordinary, but the cases detailed above are the only ones in which the dehiscence is by pores. The condition described in certain aberrant Elaeocarpaceae and Ochnaceae will be recalled in this connection.

In contrast with the preceding family, the Rubiaceae has many genera and species in which the corolla is more or less widely open and several in which it may be characterized as patent. Attention has already been called to some of these in the section devoted to the *Solanum-Cassia* type. Here we are concerned with only two genera.

The anthers of *Tresenthera* (2 species, 1 in Venezuela, the other in the West Indies), somewhat exserted from the campanulate corolla, are rather unique in their form and mode of dehiscence, opening as they do by a triangular valve below the tip. In *Rustia* (5 species ranging from Central America to beyond the province of Rio de Janeiro in Brazil) the linear basifixed anthers are of the form so generally found in apically dehiscent genera. In some species the anthers are included in the tubular portion of the corolla while in others they are exserted their entire length from the throat while the rather large lobes of the limb are patent. The occurrence of linear anthers in this genus is not so worthy of comment as in *Mendoncia*, *Pseudocalyx*, and *Hiernia* of the Acanthaceae, where the anthers are generally very short, for in the Rubiaceae the anthers are frequently linear in form and included in the corolla tube.

Too much significance must not be attached to the condition found in these genera, but it is suggestive when

compared with that of typical forms in the same family and with the typical and aberrant forms in apically dehiscent groups.

SYSTEMATIC RELATIONSHIP AND MORPHOLOGICAL CHARACTERISTICS OF APICALLY DEHISCENT FORMS.

Dehiscence by pores may be characteristic of families, genera or species. In the Rapateaceae, Tremandraceae, and, with the exception of comparatively few genera and species, in the much larger Melastomataceae, dehiscence by pores is of regular occurrence. It may be found, however, in only a few of the genera, as in *Solanum* of the Solanaceae, *Cassia* of the Caesalpinioideae, *Cheiranthra* of the Pittosporaceae and other examples which might be advanced. Probably the best illustration is the monotypic *Fissicalyx*, the single apically dehiscent genus among over 300 belonging to the Papilionatae. Only certain species of a genus, again, may have anthers with pores instead of longitudinal slits. The two Brazilian, and possibly two Indian species, of the 400 assigned to *Begonia* may be recalled in this connection, as may also three species forming the section *Leucoxylum* of *Diospyros*. The apically dehiscent habit has unquestionably been assumed independently by many unrelated genera and doubtless at various times. The regular occurrence of this method of dehiscence in several large groups indicates that in these cases the habit of dehiscence is much older, perhaps as old as the group itself. There is much to suggest that the apically dehiscent forms of the *Solanum*-*Cassia* and *Melastomataceous* types have originated from actinomorphic forms with more or less patent perianth. Evidences of exceptions to this generalization are, however, to be seen in several cases and in view of our almost complete ignorance of primitive floral types we can hardly venture to hazard any statements as to the phylogeny of these forms.

While evidence is too meager to permit of any conclu-

sions as to the type of flower from which an apically dehiscent form of any of the classes here recognized may have been derived, it seems that there is little relation between the systematic affinities of a group and the possibility of its containing apically dehiscent genera or species.

#### STRUCTURAL SIMILARITY OF MEMBERS OF THE SEVERAL TYPES.

Structurally, the apically dehiscent forms may be assembled into more or less natural and sharply limited categories. The Araceous type is a natural and sharply limited one, distinguished by a uniformity of gross structure that renders unnecessary any summary of morphological characteristics. The crowding of the anthers or their fusion into a synandrium renders apical dehiscence the most simple and the necessary mode, but the recognition of this fact does not furnish an explanation of the changes which have taken place in the development of the structure now prevailing or indicate the forces which have been active in producing them. Considerable is known of the pollination of these forms but upon the basis of the data which I have so far collected I am not yet prepared to discuss the significance of insects as a factor in the development of this floral type, or, to state the matter differently, to say in how far apical dehiscence in this type and the other structural characteristics correlated with (or determining) it are to be regarded as adaptations for fertilization by certain groups of animals. This much is certain, that the members of the Araceous type are distinct in every way from the others considered.

This last statement also applies to the Gramineous type which may also be dismissed from our further consideration.

The Polygalaceous type shows a great uniformity of structure. The locules of the short, broad anthers open



by a large terminal gap which may hardly be appropriately designated as a pore. These forms are evidently bee flowers in which the essential organs are inclosed in a ventral carina and this inclusion doubtless has a large significance in the form and size of the opening of the anther.

The Ericaceous type is one of the most important, but demands for its adequate treatment much more space than can be given to it in this place and many more data than have so far been secured. The most conspicuous characteristic of this type is the pendulous habit of the flower, with tubular, urceolate or globose corolla. In this paper, several forms which differ in the essential features from the most prevalent characteristics of the type as I have limited it have been classed with this group largely on account of their systematic affinities. The class as a whole, however, may, I think, be regarded as a very natural one.

The opening of the anther in this type varies greatly in form and size. The presence and form of the aristae on the anthers in many genera also furnish interesting characteristics and are of importance in the pollination of the flowers.

The Ericaceae are known to be largely dependent for their fertilization upon Apidae, but the epitomizing of the observations on the ecology or the geographical distribution of this large class lies outside the scope of the present paper.

The Dilleniaceous, Solanum-Cassia and Melastomataceous types must be considered together. These types are not so sharply separated as the preceding but in some degree transgressive. It is this general group of floral forms to which the present paper is devoted. The others are considered only in such detail as will show their relations, or rather the lack of any relation, to these types.

It has been impracticable to give structural details in the

preceding pages and many interesting points must be left quite untouched. Some of the major characteristics, however, seem to be significant. To these three types belong 227 genera represented by about 4,923 species. Among these the conspicuous portion of the perianth, calyx or corolla, is almost without exception campanulate or more generally widely patent and sometimes reflexed. The stamens regularly show an elongate form and are basifixed on long or short filaments. The pistil is usually simple with filiform style and small, punctiform stigma, but to this there are rare exceptions.

The Dilleniaceous type is distinguished from the others by numerous stamens and sometimes separate pistils. The number of genera assigned to this type is few. In it, dehiscence by pores seems to be the least specialized of these three types. The anthers are for the most part elongate but rare exceptions to this general rule are to be found; the pores are not infrequently continued down the sides in longitudinal slits.

In the Solanum-Cassia and the Melastomataceous types there is, as compared with the preceding, a reduction of the number of the stamens and the pistil is always simple, usually with a punctiform but sometimes slightly lobed stigma.

The minor differences exhibited by the individual genera and species of the Solanum-Cassia type are somewhat confusing but the conviction of the existence of an essential similarity in the organization of the flowers of the forms assigned to this type becomes stronger as the material is studied. Here, as everywhere else, nature seems in large measure regardless of fixed categories, and yet the structural agreement of many of these genera or species from widely separated families and of discontinuous geographical distribution — an agreement which is often so close that one would almost assert that the flowers of the several unrelated genera indigenous in the most widely separated por-

tions of the globe had been cast in the same mould or formed by the same skilled artisan—is so exact and the general structural habit of the aberrant forms is with all of the minor differences so uniform in essentials that it seems necessary to attribute it to some single factor or co-operative group of factors of environment.

Before we attempt to determine this factor, however, it will be well to assure ourselves as fully as possible of the real existence of such a structural uniformity.

Of the structural characteristics, our knowledge is fairly satisfactory, although many points can be determined only by the examinations of living material. The large series of icones, many of them executed from living material, in the library to which I have had access while carrying on this work has enabled me to make extensive comparisons otherwise impossible. It may, I think, be demonstrated beyond confutation, that the apically dehiscent forms other than the genera which have been assigned to groups designated as the Araceous, Gramineous, Polygalaceous and Ericaceous types (and all of which are, with the exception of the last, perfectly natural and sharply defined categories) may also be grouped in classes few in number and uniform in their essentials of structure.

The close structural agreement among themselves of the apically dehiscent forms assigned to any class is relatively easy of demonstration or refutation although specific variability in many genera, the presence of minor structural characteristics which tend to obscure the more essential features, and the inadequacy of our knowledge of many forms, renders this no light task.

The demonstration of a general structural similarity in all the parts of flowers, which have been brought together for comparison on the basis of a single characteristic—in the present case the mode of dehiscence of the anther—indicates that there exists a correlation between this character and the other structures of the same flower.

The nature of this correlation we cannot consider here. For the present, we are concerned only with ascertaining if an interdependence really exists. An examination of the apically dehiscent genera and species alone yields very convincing evidence in favor of this hypothesis, but theories based upon one class of data are open to criticism and especially so when the mass of material is so small as it necessarily is in the few apically dehiscent genera assigned to the Dilleniaceae or the Solanum-Cassia type.

ABERRANT NATURE OF APICALLY DEHISCENT FORMS IN  
THEIR SYSTEMATIC GROUPS.

A satisfactory kind of supplementary evidence will be furnished by a comparison of the apically dehiscent genera from the several families with the other members of the same systematic group. If in addition to an approximate conformity to the characteristics of their own type in an artificial class limited primarily by a single character, the several genera are found to be aberrant in the groups of the phylogenetic system in respect to the assemblage of their floral characteristics, we shall be justified in concluding that there is some direct and demonstrable relation between the selected character and the others pertaining to the flowers under consideration.

A thorough comparison such as that here suggested involves numerous almost insurmountable difficulties. Taxonomists are by no means agreed as to the limitations of systematic groups or as to their monophyletic or polyphyletic origin, and under these circumstances what shall serve as our basis of comparison? Not only are the limits of groups variously and oftentimes ill defined but the data available on the floral structure of species or genera are sometimes very meager. The labor involved in searching through many volumes of descriptions and figures to secure the data for such comparisons is very great and even then

the many details cannot be satisfactorily known. Few herbaria are rich enough in material to permit of an examination of a majority of the forms which should be considered and even were this the case the time and material required would in most cases be out of all proportion to the results obtained.

In making these comparisons all characters must be taken into consideration. The *Solanum-Cassia* type is not distinguished by linear, basifixed, or apically dehiscent anthers alone, or by a patent corolla, but by the association of all these characters — the patent corolla and the linear, basifixed anthers approximated around the simple style and opening by terminal pores. Excepting the essential character of dehiscence, any one of these may usually be found and often represented by a large number of genera in the family or group from which the apically dehiscent genera under consideration are taken but the combination of all the characters except that of the apical opening of the anthers in one flower is, in the systematic groups which I have examined, much more rare.

The general results of a quite detailed examination of a number of the families, are presented below: —

#### Dilleniaceous Type.

We find in the Dilleniaceae that while the numerous structural differences are very confusing it seems quite clear that apical dehiscence is confined almost exclusively to those forms with long, basifixed anthers. The presence of several free, spreading pistils in this family is unique among flowers with apically dehiscent anthers.

In the Elaeocarpaceae dehiscence may be by pores or longitudinal slits in the same genus, all genera but one having at least some species with apical pores. This single exception is *Antholoma* which has the essential floral structure of other elaeocarpaceous genera except for the gamopetalous, urceolate corolla instead of the usual polypetalous,

generally more or less campanulate, perianth of other representatives of the family. The stamens in this family are usually linear and basifixed on filaments of varying but usually considerable length and, in this respect, conform to the ideal type of this class.

Elongate, basifixed, usually apically dehiscent anthers are characteristic of the Ochnaceae. Other points will be taken up under the Solanum-Cassia type to which the most of the representatives of this family have been assigned.

Of the Theaceae my knowledge is insufficient to permit of comparisons.

*Bixa* of the Bixaceae is an anomalous form.

#### Solanum-Cassia Type.

Turning now to the Solanum-Cassia type we find material which yields more satisfactory results.

The Mayacaceae is monotypic and its relationship is not so evident as to justify comparisons of its floral structure with that of other families.

All of the genera of the Rapateaceae are apically dehiscent. The family is considered most closely related to the Xyridaceae and Eriocaulaceae.

A patent perianth is characteristic of the Commelinaceae and, except for a slight elongation of the anthers, the apically dehiscent genera do not differ essentially from some others to be found in the family. At the same time the various structure of the anthers and the filaments of many of the genera distinguish them at once from the apically dehiscent forms.

In the Pontederiaceae, *Monochoria*, the anthers of which open only at first by apical pores which are soon continued down the sides in slits, has the corolla tube most reduced and the limb more widely patent than any forms except some species of *Heteranthera* with a long tube. The filaments and anthers are of about equal length, but the

anthers have probably the greatest relative length in the family.

The floral structure of the Liliaceae and Amaryllidaceae is hardly to be summarized in general terms. We may, however, repeat that in the Amaryllidaceae the prevalent habit of the perianth may perhaps best be described as infundibuliform, while in the Liliaceae it is more frequently patent or campanulate. In the Amaryllidaceae the four apically dehiscent genera stand almost alone as representatives of the Solanum-Cassia floral habit while in the Liliaceae there are many genera with patent or broadly campanulate perianth and in some of these the filaments are reduced in length, and the anther is of the more elongate form commonly seen in the apically dehiscent genera.

*Sollya* and *Cheiranthra* are quite aberrant forms in the family Pittosporaceae in which they belong, both as regards form of perianth and structure of stamens.

In the Leguminosae the apically dehiscent genera belong to a group in which the perianth is generally patent, but they differ in the relative length of the filament and anther and in the insertion of the anther upon the filament.

The Tremandraceae contains only apically dehiscent genera and species.

The sterculiaceous genera which have been mentioned as having anthers opening at least at first with pores are marked by a great similarity of structure, a greater similarity than that between the apically dehiscent genera and the other genera of the Lasiopetaleae, to which all of the apically dehiscent genera belong, in which the anthers open from the first by longitudinal slits. The Lasiopetaleae itself differs very essentially in its floral structure from other tribes of the Sterculiaceae so that there can be no question as to the unique structure of these forms in this family.

The Ochnaceae has the elongate, basifixed anthers of the Solanum-Cassia type and most of the genera have anthers

which open at least at first by terminal pores. Since the floral habit of this family conforms to that of our Dilleniaceous and Solanum-Cassia types, the only opportunity for comparisons is between the genera which may be assigned to these two types and certain aberrant forms to be mentioned below. We may postulate that the Solanum-Cassia type has in some cases been derived from the Dilleniaceous type by a numerical reduction of the androecium accompanied in most instances by a shortening of the filaments. On the whole, dehiscence by pores seems to be more perfected in the Solanum-Cassia type. A family containing representatives of both types should furnish data of value for a study of this question but, as pointed out above, the evidence available in the present case is too meager. A strong reduction in the androecium has clearly taken place so that the family is broken up into more than one floral type, but whether this reduction occurred entirely subsequent to the development of the apically dehiscent habit or whether it largely preceded it is a question which cannot be easily decided. The anthers of some species of this family which have been assigned to the Solanum-Cassia type show no more specialized apical dehiscence than some which have been assigned to the Dilleniaceous type. On the other hand it is to be noticed that certain genera are very suggestive of the Melastomataceous type—a group of forms the evolution of which has apparently progressed along a very different line from that of the Solanum-Cassia type—and this may explain the equal perfection of apical dehiscence in forms with numerous stamens with long filaments and in those with few stamens with short filaments.

In certain anomalous genera the staminodia are so modified as to form a more or less perfected tubular or urceolate corona. In these genera, the anthers open by longitudinal slits and since the same condition prevails in other genera with an urceolate perianth in families in which the perianth is usually patent and the dehiscence apical, it seems legiti-



mate to conclude that the exerted condition is a factor of importance in the development or permanence of the apically dehiscent anther. Comparative evidence would suggest that these forms with cylindrical or urceolate perianth are not primitive, but of recent origin. The anthers seem to open at first by a terminal gap and it may be that longitudinal dehiscence has been reassumed by these forms as a result of the changes in the form of the perianth.

Only a thorough knowledge of the living plants in their own environment supplemented by histological studies will decide some of these questions.

*Stemonoporus* and *Monoporandra* differ in the structure of the androecium from all other Dipterocarpaceae.

In *Begonia* the perianth is patent in all forms. The two apically dehiscent species of the section *Solanthera* have more elongate anthers than many species of the genus, but the distinction here is not a very sharp one.

The structure of *Gardneria* seems to be unique among the Loganiaceae.

In the Gentianaceae a few forms approach very closely the structure of the apically dehiscent genera and many agree in some characteristics, but on the whole it seems to me that *Exacum* and *Cotylanthera* depart markedly from the type of the family.

A long corolla tube is characteristic of most Solanaceae. Several genera have a more or less widely open corolla. Among these, *Solanum* is the genus in which the anthers have attained the greatest length and the filaments are most reduced.

Comparisons in the Rubiaceae are rendered very difficult by the size of the family, the inadequacy of our knowledge of the floral structure and especially by the large number of genera which show some of the characteristics of the flowers of the *Solanum-Cassia* type; but when all characters are considered, *Argostemma*, *Neurocalyx* and *Strumpfia* seem to be unique in this vast family.

## Melastomataceous Type.

In the Melastomataceous type, the Melastomataceae need not engage our attention here. We have already noticed the similarity of floral structure in the Melastomataceae. The floral structure is quite unique and a comparison with groups to which it is more or less closely related is not possible in this place.

The essential structural difference between the Solanum-Cassia type and the Melastomataceous type seems to be the length of the filaments. The long filaments make possible the highly organized anthers found in the latter. The structure of the flowers need not be redescribed here. The essential similarities may be gathered from any series of descriptions or plates of the genera of this family, while the minor details are too numerous and perplexing for consideration.

The species from other families which have been assigned to this type are very few. *Storckiella* is the only genus of the Cassieae with elongate filaments. *Maximiliana* and *Amoreuxia* of the Bixaceae have the form of anther which is so frequently seen in this type and long, filiform filaments. The stamens are more numerous than is usually seen in the Melastomataceae. The Bixaceae comprises four genera belonging to three tribes. The first contains the unique *Bixa*, the second *Maximiliana* and *Amoreuxia* and the third *Sphaerosepalum*, exhibiting numerous stamens with long, filiform filaments and nearly globose, dorsifixed, versatile anthers dehiscing by longitudinal slits. The structure of the two genera which I have assigned to this type is, then, quite unique in this family.

As I have insisted above, the limitation between the Solanum-Cassia and the Melastomataceous type is not a sharp one and it may be that such forms as *Cheiranthera* of the Pittosporaceae and *Exacum* of the Gentianaceae would have been best treated under this type. Here, a

knowledge of the living plants such as may be gathered by those who know them in the field is most desirable.

#### RECAPITULATION.

The evidence assembled in the preceding paragraphs seems to point clearly to certain easily stated conclusions. Not only do the apically dehiscent forms show a high degree of similarity *inter se* but the several forms are very frequently aberrant in respect to the totality of their characters in the systematic groups to which they belong. In other words, apical dehiscence of the three types here considered occurs only in flowers of a certain structural habit. The objection which might be raised that I have included in these three groups only such forms as *are* similar in the totality of their characters is disarmed by the fact that these three classes are sharply distinguished from the first four types recognized and that anomalous forms are very few. The fidelity to type of the apically dehiscent genera and in many cases their aberrant floral habit when compared with other members of the same systematic group speak strongly in favor of a correlation between the floral parts and the form and mode of dehiscence of the anther. The exact significance to be assigned to the broad term correlation must be defined in each case if ambiguity is to be avoided. Interdependence of parts may be real or apparent, due to internal or external forces. In this paper, I have sought to avoid all theoretical considerations and I shall not discuss the nature of the correlation observed in these forms. I have used the term in the broadest sense, indicating any reciprocal relationship of parts; the ground for the assumption of such a relationship is found in the constancy with which the characteristics in question are found associated in the apically dehiscent forms.

## FLORAL ECOLOGY OF APICALLY DEHISCENT FORMS.

It was the similarity of adaptation which first aroused interest in the morphological peculiarities described above. We may now examine the data available upon these floral structures regarded as adaptations.

The ecology of the Araceous, Gramineous and Polygalaceous types is quite foreign to our present considerations. That of the Ericaceous type has many points of interest but material is not yet satisfactorily arranged for a summarized statement and the individual data are too numerous for consideration here.

## ECOLOGY OF DILLENIACEOUS TYPE.

In the Dilleniaceae, Ducke saw *Melipona bipunctata* abundant on an unidentified *Tetracera* at Para in Brazil and also a small species of *Halictus* visiting the flowers of *Davilla rugosa* in great numbers. On *Saurauia* the interesting habit of producing inflorescences from the lower regions of the main stem has been described in some detail. Knuth observed in Java numerous small insects upon the flowers of *S. cauliflora*: "Vor allem war Thrips sehr häufig in den Blüten, Musciden flogen unet von Blüte zu Blüte und hielten sich in jeder einzelnen mehrere Sekunden auf, mit grossen Ballen weissen Pollens wieder hervorkommend, und auch kleine Bienen (*Podalirius?*) flogen ab und zu." As a visitor of *S. nudiflora* he saw *Podalirius* clinging to the flowers from below and diligently collecting pollen. It is unfortunate that the evidence is so meager that one is only able to surmise that these are pollen flowers, perhaps very similar to *Rosa*.

Observations on the Elaeocarpaceae are of the characteristic meagerness. According to Thomson, *Elaeocarpus Hookerianus* of New Zealand has perfect, white, protandrous flowers in which a glandular ring at the base of the stamens secretes nectar freely; it appears to be entomophil-

ous. Dahl saw the honeyless (?) flowers of *E. Pankinsoni* visited by two birds — *Charmosyna* and *Myzomela* [for what purpose?]. In *Aristotelia Maqui* there are said to be bright yellow male flowers with two whorls of stamens and smaller physiologically female flowers with one whorl. In Chile Johow found the flowers industriously visited by the honey bee.

In New Zealand according to Thomson *A. racemosa* shows transition stages from hermaphrodite to purely staminate or pistillate flowers. These are red and destitute of odor or nectar; the light, pulverulent pollen suggests anemophily. *A. fruticosa* of the same region has polygamous flowers which lack odor and nectar, but here anemophily is doubtful.

The unique form of the anthers and perianth in the Elaeocarpaceae renders a fuller knowledge of their floral ecology highly desirable.

On the large, red flowers of *Bixa*, of the Bixaceae, Ducke observed at Para the females of several species of bees belonging to *Centris*, *Euglossa*, *Bombus*, *Xylocopa*, *Melipona*, especially large species, and *Halictus*.

#### ECOLOGY OF SOLANUM-CASSIA TYPE.

Fortunately our knowledge of the floral ecology of the members of the Solanum-Cassia type is much fuller and so it will not be so necessary to cite the special observations as it has for the Dilleniaceous type.

Delpino divides the twelfth class (Apparecchi prensili) of his biological classification of floral forms into two types, "Tipo Boragineo" and "Tipo Verbascino." The first of these is of very particular interest in this place since the Solanum-Cassia type as limited in this paper is, so far as observations and conclusions from analogy go, very nearly synonymous with it.

The Borago floral type is, according to Delpino, characterized by pendulous or quasi-pendulous flowers. The long

anthers, inserted on short, thick filaments, are connivent in a cone, through the center of which passes the style. Dehiscence is at the apex by pores which may be continued longitudinally. The pollen is dry and smooth, and necessarily falls upon the ventral surface of the visiting insect at the moment when it grasps the staminal pyramid. In order that the insect may cling to the staminal column the expansion of the flower is generally considerable. Nectar is absent or present only in small quantities. In the former case the bee collects only pollen. This type is exclusively melittophilous, “e sorprendentemente si ripete co' suoi essenziali caratteri in molte famiglie di piante, cioè' nelle *Boraginee*, *Primulacee*, *Solanacee*, *Scrofulariacee*, *Amarillidee*, *Asparaginee*, *Pittosporee*, *Loasacee*.”

In this type he places, with comments upon many forms, *Borago officinalis*, *Cyclamen europaeum*, *C. coum*, *C. persicum* and other species, *Dodecatheon Meadia*, *D. integrifolium*, *Solanum Dulcamara*, *S. nigrum*, *S. tuberosum*, *S. Lycopersicum*, *S. insanum* and many other species of the genus, *Verbascum Myconi*, *Galanthus nivalis*, *Leucjum vernum*, *Conanthera bifolia*, *Cajophora lateritia* and many species of *Loasa*, *Sollya linearis*, *Dianella coerulea* and other species of this genus.

Delpino's division of floral forms into fixed categories has been censured, and one of the most severe criticisms by Müller refers to this type. Without intending an evaluation of the classification as a whole I must say that it seems to me that Delpino's generalizations for this type have been very satisfactorily substantiated by the observations which have been accumulated since his essay appeared. In their relations to insects the forms which are here placed in the *Solanum-Cassia* type are in close agreement with Delpino's *Borago* type. For the purposes of this paper the classification is extended so as to include the zygomorphic forms so common in *Cassia* and occurring in

some other genera, forms which should perhaps be placed in the Melastomataceous type as Delpino has done. It must be recognized, however, that between these types there is no sharp distinction and that the groupings adopted are merely for the purpose of more convenient comparisons. In treating the floral ecology of the Solanum-Cassia type it seems best to discuss in some detail the two type genera and compare with them other members of their respective families, taking up afterwards the other forms in their systematic sequence.

We may first consider briefly the actinomorphic Solanums.

*S. Dulcamara* has been most thoroughly studied. It belongs clearly to Delpino's *Borago* type. The Syrphidae and Lepidoptera observed as visitors by Müller must be regarded as accidental or insignificant. According to most reports, *S. Dulcamara* is little visited, but Hoffer found the visitors in one locality very abundant and active, no less than seven species of *Bombus* and one of *Osmia*, as well as *Rhingia*, *Volucella* and *Argynnis* being observed. *S. nigrum* and *S. Carolinense* have been observed to be sparingly visited by *Bombus*. On *S. elaeagnifolium* at Las Vegas, N. M., Cockerell took eighteen species of Apidae belonging to fifteen different genera. At Para, Ducke observed as visitors of *S. grandiflorum* (said in systematic works to have a violet corolla  $2\frac{1}{2}$ –3 inches in diameter) one species each of *Oxaea*, *Xylcopa*, *Bombus* and *Halictus* and six of *Centris*. At the same place he observed one species of *Halictus*, seven species of *Euglossa* and a large species of *Melipona* visiting the flowers of *S. toxicarum*. On an unidentified species with blue flowers he records only species of *Melipona*, especially *M. fasciata*, *Bombus cayennensis* and *Halictus*.

Darwin reports observations by F. Müller on *S. pollinacanthum* at Sta. Catharina, Brazil. He found it visited ex-

clusively by pollen collecting bees, *Melipona*, *Euglossa*, *Augochlora*, *Megacilissa*, *Eophila* and others.

I have observed that *S. sisymbriifolium* has a very pronounced perfume, suggesting more abundant insect visits than in many other species in which no fragrance is to be detected. In the summer of 1903, I found large bees with the greatest frequency collecting pollen. In his paper on Brazilian solitary bees Schrottky gives *S. Balbisii* (= *S. sisymbriifolium*) as one of the principal flowers visited by *Xylocopa*.

Though few, these observations indicate clearly the true method of pollination in the actinomorphic species of this large genus. A few species are zygomorphic. Upon two of these, direct observations have been made. Both have been shown to be exclusively adapted to pollination by the larger bees, *Apis* and *Bombus* having been observed as well as some of the smaller Apidae. The numerous interesting points incident to their zygomorphy and their accompanying lateral asymmetry cannot be detailed here.

Between the zygomorphic Solanums and Cassias a most remarkable ecological similarity prevails and it was this which first called attention to the problem in hand.

The floral ecology of the genus *Cassia* has attracted considerable attention, the first suggestive observations being those of Delpino and Leggett in 1871 to 1881. The paper by Todd on *Solanum rostratum* and *Cassia chamaecrista* called particular attention to both of these genera and has been the incentive to most of the later work. The more important papers are those by Todd, Müller, Burck, Harris and Kuchs and the recent treatment in the third volume of Knuth's Handbuch.

Since the appearance of Todd's paper and the more general one by Müller the attention of writers has been chiefly devoted to the "division of labor" in the stamens and the curious phenomenon of right- and left-handedness, or enantiotyly as it has been called.



These morphological features of *Cassia* may not be discussed here although they have figured conspicuously in all the ecological discussions pertaining to these genera. Their true significance has probably not yet been correctly interpreted.

On *C. chamaecrista* in Iowa Todd saw a small humble bee. In Illinois Robertson observed four species of *Bombus* collecting pollen. "Landing upon the anthers, they seize them between their mandibles and stroke them downwards with a sort of milking motion." In a later paper he states that the flowers are visited by the pollen collecting female of the oligotropic *Podalirius walshii*. In eastern Kansas, Harris and Kuchs observed one species each of *Apis*, *Agapostemon*, *Melissodes* and *Bombus*. Near St. Louis I have observed *Bombus*.

According to the observations made by Meehan, Robertson and myself, *C. Marylandica* is visited by *Bombus*. Pollen is collected only from the smaller upper stamens, the three lower ones serving the insect only as a supporting platform if at all. Flowers protected against insect visits do not produce fruits. The pollen from the large lower or the three smaller upper stamens, may effect fertilization, but whether there is a difference in the efficiency of that from the two kinds of stamens is not known.

In an unidentified species from Brazil related to *C. laevigata* Fritz Müller observed *Bombus violaceus* and species of *Centris* collecting pollen from the short, central anthers while the two long, lower anthers and similarly shaped pistil are so much curved as to strike with the anther tips and the stigma the dorsal surface of the abdomen of the visiting insect. The large, lower stamens are of the same color as the smaller, central ones and were observed to be visited extensively by small insects which despoiled them of their contents without effecting pollination: *Trigona elegantula*, *T. lilliput* and a large

species of *Augochlora*. *Trigona ruficrus* often bites the anther quite in pieces.

Burck considers that the floral mechanism of *Cassia* favors autogamy, basing his conclusions on the fact that in several species studied by himself the tip of the pistil returns to the median plane of the flower by a new curvature of the style so that it will not come in contact with the region of the insect's body previously supplied with pollen from the pores of the larger stamens, and that in others the stigma comes almost in contact with the tips of the stamens.

Burck's paper contains some interesting observations, but it seems that his conclusions can hardly be accepted without further investigation. For a more detailed comparison of his statements and conclusions, reference must be made to his own paper.

According to him, *C. glauca* differs from the other species in having coriaceous instead of indurated anther walls. The large bees — *Xylocopa* and *Bombus* — which visited this, and other species observed by him, alight in the middle of the flower and "devour the grains of pollen" of the five short stamens or they may destroy in part or entirely both the anther walls and the pollen. Only the two large stamens remain intact and undespoiled of their pollen. Knuth's observations on *C. Horsfeldii*, considered by some a synonym of *C. glauca*, confirm Burck's observations on this point. The bee flies directly towards the small stamens, grazing but rarely the large anthers; when these are touched, it is with the ventral surface of the body. He never saw the stigma in contact with the body of the visiting insect but thinks that this might occur, especially at the moment when the insect leaves the flower. But even then, the chances are that the dorsal surface of the insect's body, rather than the ventral surface to which the pollen adheres, will touch the stigma.

The significance of the elongation of these lower anthers

is, he thinks, their protection from the insect visitors. According to the observations of O. Schmiedenknecht this species in the garden at Buitenzorg is visited principally by species of *Ceratina*. *C. bacilluris* has indurated anthers, so that, according to Burck, the insect can secure pollen only by inserting its proboscis into the terminal pores. Knuth speaks of the anthers being so completely milked out that only a few grains remained. In the Buitenzorg garden, 4 species of *Xylocopa* and unidentified Syrphidae were observed as visitors.

*C. alata* has been described by Burck, Lindman, Ducke, and Knuth. Lindman saw large and small bees visiting this form in large numbers. He states that in this species, as also in *C. aculeata*, the large anthers sometimes contained no pollen even in the bud. Ducke saw at Para and Macapá, 4 species of *Centris*, 3 of *Xylocopa* and 4 of *Euglossa*. At Buitenzorg, *Ceratina* was the principal visitor observed.

Some of the species studied by Knuth at Buitenzorg have already been mentioned. We may summarize his observations on the other species by saying that he usually found only *Xylocopa* as a visitor. In rare cases he observed *Podalirius zonatus* and *Megachile opposita*. *Centris* and *Euglossa* do not occur there. O. Schmiedenknecht also observed several species of *Ceratina* on *Cassia* flowers at Buitenzorg. Knuth thinks that cross fertilization is favored since the projecting stigma will be touched first by a visiting insect. In all cases supplementary self-pollination may occur when the flowers are visited by bees, but spontaneous autogamy he considers possible only in the species with small flowers which close after a time, bringing the stigma into immediate contact with the anthers. In St. Louis, I have taken *Bombus* and smaller bees collecting pollen from *C. sophera*.

According to Müller, *C. multijuga* at Blumenau, South Brazil, is visited by *Xylocopa artifex* and another large,

apparently undescribed species, and by *Centris lineolatus*.

Trelease saw *C. obtusifolia* visited by *Bombus* in central Alabama.

Schrottky observed *Centris discolor* regularly collecting pollen on *C. splendida* at S. Paulo, Brazil. Here he also saw species of *Centris* collecting the pollen of *C. bicapsularis*.

At Para, Ducke observed on *C. Hoffmansegii* and other species with very large flowers, *Xylocopa*, *Centris*, and *Euglossa*.

In Chile, Johow saw *C. closiana* visited by *Bombus chilensis*.

In Chile, Darwin saw a *Mimus* with its head yellow with pollen, from, as he thought, a *Cassia*. Delpino records *Cassia* (?) as visited by *Nectarinia platura*. Fries once observed *C. bicapsularis* visited for insects by *Chlorostilbon auriventris*. He found the species regularly visited and pollinated by *Bombus carbonarius*.

Our knowledge of forms other than *Solanum* and *Cassia*, is, so far as direct observations are concerned, very fragmentary. Brown studied the flowers of *Labichea lanceolata*, and, finding the same right- and left-handed arrangement as in *S. rostratum*, concluded that the method of pollination is the same. It can hardly be doubted that the other forms of the Cassieae are, at least for the most part, dependent upon the larger pollen-collecting bees for their fertilization.

On the ecology of the Mayacaceae and Rapateaceae no observations have been published.

Of the floral ecology of the Commelinaceae under consideration we are quite ignorant. I have been able to examine living material of one species of *Dichorisandra* and to convince myself that there is no secretion of nectar. The ecology of the flowers of some genera of the family is quite well known, and comparative evidence makes it very

probable that most of the Commelinaceae are without nectar and are visited by pollen-collecting bees.

Before leaving this subject, I will refer briefly to the anomalous *Cochleostema*. It is the most magnificent member of the Commelinaceae, with flowers two or two and one half inches in diameter, sepals and petals highly colored and patent, androecium of six elements in two whorls, fertile stamens 3, 1 from outer and 2 from inner whorl, forming a pedicelled staminal column with the anthers all spirally twisted and dehiscing longitudinally; one horizontal at the base of a corniform hood formed by involute, petaloid outgrowths from the other two which inclose all three stamens.

The habit of this most complex flower is almost exactly identical with that of some of the zygomorphic, apically dehiscent forms, as for instance, *S. rostratum*, the form of the perianth and the position of the pistil being the same and the staminal hood simulating almost exactly the arcuate anther. Loew and Appel in Knuth's Handbuch devote considerable space to a discussion of this remarkable plant and I shall add the further suggestion that the fragrant, nectarless flowers may be adapted to the larger Apidae which seek the hairs of the staminodia or other juicy portions of the flower and effect pollination in the same way as in apically dehiscent forms.

When I first saw a habit figure of *Cochliostema* I thought it an apically dehiscent form with one large anther similar to *S. rostratum*. If the suggestion just offered prove the right one, we have a most remarkable case of parallel adaptation.

Nothing is known of the pollination of *Monochoria*. *Pontederia* is visited for nectar and sometimes for pollen by large bees. *Heteranthera* has been described as a pollen flower. The secretion of nectar is not abundant if it occurs at all in *Eichornia*, at least when grown in the north. On *E. azurea*, Müller observed only bees belonging to the

genera *Melipona* and *Anthophora*. I am inclined to believe that in *Monochoria* we have a highly developed pollen flower, connected by various stages with other members of the family showing a deep nectar bearing tube.

In the Liliaceae, all forms of which, with the exception of the aberrant *Odontostomum*, belong to the Solanum-Cassia type, zygomorphy is not so pronounced as in several other families, the Amaryllidaceae for instance, apparently only *Agrostocrinum* having a zygomorphic habit. The flowers are all of a good size and usually highly colored, the anthers quite often in sharp contrast with the perianth. Thomson states that *Luzuriaga parviflora* has white, fragrant pollen flowers! Delpino considers *Dianella coerulea* and other species as pollinated in the same way as *Borago* or *Solanum*.

In the Amaryllidaceae, direct observations are wanting, but the zygomorphic condition of *Zephyra* and *Tecophilea* and especially of *Cyanella* indicate ecological relations similar to those of the zygomorphic Solanums or Cassias.

Nothing is known of the ecology of the two representatives of the Pittosporaceae considered, but their structure is so similar to species which are well studied biologically that there can be little doubt as to their insect visitors. The little that is known of other genera indicates a wide difference in the insect relations of the typical and the aberrant members of the family.

The Tremandraceae are doubtless entirely dependent upon pollen-collecting bees for cross fertilization. This cannot be said with the same confidence of the Sterculiaceae considered above, but from the structure of some of the forms it seems not improbable that they are visited and pollinated in the same manner as *Solanum* or *Borago*.

Gilg considers that in the absence of direct observation it is to be assumed without question that the flowers of the Ochnaceae are insect pollinated. The magnificent flowers, the zygomorphic disposition of the anthers in some species,

especially the peculiar condition of the anthers connate in masses in *Luxemburgia*, and the pleasant odor observed for others (the odor of violets in *Schuurmansia Henningsii*) all speak strongly in favor of this conclusion. Visitors are recorded for but one species. Ducke observed *Xylocopa barbata* visiting the flowers of an unidentified *Ouratea*.

Of the method of pollination of the Dipterocarpaceae we know nothing, and can only surmise from the structure of the flowers. The same is true of the Flacourtiaceae under consideration.

Nectar has never been demonstrated in the showy but usually odorless flowers of *Begonia*. Warburg noticed numerous small insects visiting the flowers in their native habitat. On an undetermined Javan species Knuth observed *Apis*, *Bombus* and *Podalirius* (presumably collecting pollen.)

Of the Myrsinaceae and Loganiaceae in question we know nothing.

Mr. J. C. Willis, Director of the Royal Botanic Gardens, Peradeniya, kindly sends me the following note on *Exacum* of the Gentianaceae: "The only Melastomaceae I have actually seen pollinated yet are our common big pink Osbeckias, which are visited by the big carpenter bee, *Xylocopa*, sp., apparently for pollen. The bee pollinates our big blue *Exacum macranthum*, which looks just like a Melastomaceae. It squats down on the flowers and bunches up the stamens with its legs, and must get lots of pollen jerked out of the apical pores onto its body. In fact I have usually found flowers visited by it to have the stigmas well pollinated, and have hardly ever seen any other insect visit them at all. There is little or no honey, so far as I have noticed, in these flowers or in those of Melastomaceae."

*Solanum* has been discussed above. I have been able to examine one species of *Cyphomandra* in a living condition. There appears to be no free nectar. The walls of

the anthers are thin and elastic so that the pollen is ejected by a bellows-like action as in some Melastomataceae.

Of the Rubiaceae we know nothing.

#### ECOLOGY OF MELASTOMATACEOUS TYPE.

As one glances over the icones of the numerous genera he is impressed with the high degree of organization and the splendid colors, often heightened by the marked contrast between the androecium and the perianth, of the flowers of the Melastomataceae. The natural conclusion is that these represent forms dependent in high degree upon insect visitors. It is very disappointing that our knowledge of the floral ecology of these forms is so meager.

Ule remarks: "In vielen Fällen scheint es bei den schönblühenden Melastomaceen nur darauf anzukommen, dass die Staubgefässe in Bewegung gesetzt werden, und deshalb stehen sie auch noch auf einer niederen Stufe der Anpassung an Insektenbesuch. Der Mangel an Insekten, welche die Blüthen der Melastomaceen aufsuchen, verursachte wahrscheinlich das intensive Farbenkleid mit dem viele die Gegenden zu Zeiten schmücken, wie es keine andere Pflanzenfamilie in Brasilien thut. Ich erinnere hier an andere auffallende und grosse Pollenblumen, wie z. B. *Papaver*, *Tulipa*, *Rosa*, etc." Ducke says of the family at Para: "Es ist auffallend, dass diese hier so artenreiche Familie nur sehr wenig von Apiden besucht wird; höchstens findet man ab und zu *Halictus* an diesen Blüten. Nur eine baumartige Melastomacee sah ich hier öfters von Hummeln (*Bombus cayenensis*) umschwärmt."

Leggett first described the bellows-like action of the stamens of *Rhexia Virginica* and observed *Bombus* visiting the flowers. Unfortunately he does not state whether nectar is present. According to Bailey the pollen of *Heterocentron roseum* is ejected in the same way. According to Müller and Forbes certain species of *Melastoma* and *Heeria* agree in the essentials of their floral mechanism.



The flowers need not be described here in greater detail than to state that the larger lower anthers are of the same color—violet or red—as the vertical patent corolla, against which the shorter, bright yellow, central stamens form a striking contrast. Müller observed only a small fly (Syrphidae) collecting pollen from the yellow anthers and *Trigona ruficrus* visiting first the small anthers and then often the larger ones, offering a more generous pollen store, as well, working on them with their mandibles and often devouring them entirely. Forbes speaks of the pollination of such forms as follows: “I have witnessed in many instances the visitation by various species of large Hymenoptera, such as *Xylocopa* and *Bombus*, of species especially of the genus *Melastoma*, possessing stamens in all points corresponding to that occurring in the *Heeria* described in the letter referred to, and what takes place seems to be as follows. The large bees evidently make for the yellow platform offered by the short stamens, perhaps because they do not perceive the pistil and long stamens owing to their projection against the broad petaled corolla of the same color in the background, and invariably receive the pistil between their legs, their feet settling on the fork of the connective, the instant effect of which is to collect the whole of the long stamens into a bunch, and to depress their anthers downwards and away from the body of the visiting bee, while the pistil remains in constant contact with its ventral side. At the moment of the bee’s departure the hooks on the bee’s feet by pulling on the connective fork, raise the anthers of the long stamens, so as to bring the tips of the collected bunch into contact with its sides and abdomen. Dr. Müller’s statement ‘by moving the connective fork of the larger ones’ is somewhat ambiguous; for it is movement only in one direction that is of avail in *raising* the anthers of the larger stamens, pressure at the connective hook of course tends to depress the anthers and keep them apart from the

bee's abdomen while a very slight backward pull at once raises the anther."

Forbes and Burek were able to detect differences in the pollen of the two types of stamens. "The pollen from the short stamens was large and three-cornered, while that of the longer ones was very much smaller and of a more oval shape; and while both forms were found on the pistil, only the pollen from the long stamens seemed to be fertile. We could not detect any of the short-stamened pollen with tubes opened." In a later paper Forbes records *Bombus senex* as a visitor. In his paper on division of labor in the stamens of pollen flowers, Müller records further observations by his brother in which incipient stages of the color dimorphism were observed in a melastomataceous genus, probably *Pleroma*. The significance of color dimorphism has already been alluded to under the *Solanum-Cassia* type.

Ule studied some species of *Tibouchina* for comparison with *Purpurella*. The visitors of these flowers with splendid colors he found relatively few while they were much more active on the inconspicuous flowers of *Croton*, *Spermacoce*, *Sida*, etc., growing near by. Butterflies, flies and birds do not visit these forms which secrete no free nectar but offer only pollen difficult of collection which various pollen-collecting Hymenoptera are able to gather. The pollen is not so dry as in *Purpurella* but a little sticky. A few times he saw humble-bees visiting the flowers, and once he was able to examine in detail the action of one on a shrub of *T. Moricandiana*, "die immer schnell den Kopf noch dem Mittelpunkt der Blüten steckte und bald einen Strauch abgeernt hatte. Warscheinlich fängt sie so den ausspritzenden Blütenstaub in den Haaren auf und kann dann leicht Fremdbefruchtung erzeugen. Häufiger sind kleine und winzige Bienen, welche die dünne, gefaltete Antherenhaut durchnagen und so den Pollen einsammeln, wie ich mich öfter überzeugt und sogar die

Bienen mit ihrem pollenbeladenen Höschen eingefangen habe. Bei dieser Arbeit verweilen diese Bienen allerdings längere Zeit in jeder Blüthe." Another group of insects attack the stamens and sometimes devour them entirely, and he often found large wasps on the flowers of *T. gloriosa*, while in this class are also to be placed Coleoptera, as species of *Cytonia* and *Buprestis* which are especially to be sought in the handsome flowers of the Melastomataceae. The attractiveness of the stamens for insects and the secretion of nectar by these organs in *Purpurella* led to a microscopic examination of these parts of *T. gloriosa* with the demonstration of an abundance of sugar which, however, is never excreted in visible form. In many species of *Tibouchina* a pronounced change in color in different ages of the flower is demonstrable, and of this several examples are given.

A note from Mr. Willis on the pollination of the Melastomataceae and *Exacum* has been quoted above under the Solanum-Cassia type.

From the detailed discussion by Lagerheim, *Brachyotum ledifolium* seems to be adapted to pollination by birds. The depth of the nectar and the size of the opening in connection with the consistency of the perianth and the position of the flower tend to exclude insect pollinators with the exception of the Sphingidae, and these are hardly to be considered on account of the lack of perfume in the flowers and the insufficiency of a soft proboscis for the ejection of the pollen from the anthers. As visitors he observed *Rhamphomicron herrani* and *Metallura tyrianthina*. These inserted their beaks into the small opening of the flower for the purpose of obtaining insects or nectar secreted by the filaments and forced a puff of pollen from the bellows-like anthers by pressing them with the tip of the beak. By pressing the elastic anther wall with a rounded match the pollen may be ejected for a distance of three centimeters, after which the wall assumes its original

position and the pollen collects in the small portion of the anther until by repeated compressions it shall all have been ejected. The stigma projects beyond the anthers and so is first touched by the visiting bird. Presumably other species of the genus are also ornithophilous, but *B. Benthamianum* would seem from the floral structure to be dependent upon bees for pollination.

Very interesting observations were made by Burck upon *Memecylon edule* var. *ramiflorum*. He describes the prominent, active, yellow nectary on the dark violet connective spur. He finds the flowers well protected from a large destructive ant by smaller ones which secure nectar secreted from the outside of the calyx tube, but not from the staminal glands. As pollinators he found small, active flies such as are concerned in the pollination of *Aristolochia*. These flies do not seem to fear the ants and he suggests that after the flower had developed in adaptation to bee visitors, these found the more recently arriving ants uncongenial, and upon their desertion of the plant another adaptation to insects of a very different type became necessary and then the recent staminal nectaries arose.

As pointed out in the descriptive portion of this paper, the disposition of the petals in the Melastomataceae is very rarely campanulate. One such form, *Brachyotum*, has been described above. In *Purpurella cleistopetala* from the Serra do Itatiaia of Brazil, as described by Ule, the flowers never open. The discussion of structural points need not be repeated here. He at first suspected that *Bombus* was the insect concerned in pollination, but repeated observations revealed only a small ant covered with pollen. A larger species of ant destroys the flowers. Other forms found in the mountains, as *P. hospita*, have pendulous campanulate flowers.

According to Darwin *Centradenia floribunda*, *Rhexia glandulosa*, *Monochaetum ensiferum*, *Heterocentron Mexicanum* and species of *Pleroma* are self sterile or but rarely

produce fruit when left to themselves, but produce seed abundantly when artificially self fertilized.

Little is known of forms outside the type family. Ducke observed *Centris* and *Xylocopa* visiting the magnificent golden yellow flowers of *Cochlospermum* (= *Maximiliana*) *insigne* but nothing is recorded concerning the objects of the visits.

#### RECAPITULATION.

Summarizing this section, we may say that our knowledge of the ecology of these forms is far from satisfactory. Our acquaintance with the ecological relations of the Dillenaceous type justify no conclusions, but for the Solanum-Cassia and the Melastomataceous types nearly all the direct observations which we have and the entire mass of comparative data indicate adaptation to the Apidae and among these, for the most part, to those which are active in the collection of pollen. The absence of nectar practically limits the range of visitors to pollen-feeding flies and pollen-collecting Apidae. The evidence for adaptation to the latter is very great. As to the origin or method of evolution of these types of adaptation, our evidence will not justify any conclusions, but of the reality of their existence, we may have a high degree of confidence.

We must now leave this phase of the subject which I hope to take up briefly again after considering the data of two other sides of the problem.

#### THE GEOGRAPHICAL DISTRIBUTION OF APICALLY DEHISCENT FORMS.

In the introduction to this paper, it was suggested that the flora of certain regions is richer in apically dehiscent forms than is that of others. The examination of this hypothesis was one of the principal objects of the investigations described.

The Solanum-Cassia type seems to be the one best adapted for a first study of this question.

Of the Monocotyledons one family, the Rapateaceae of 6 genera, is endemic in tropical South America. *Mayaca* has 8 of its 10 species there. Of the two apically dehiscent Commelinaceae, the genus in which dehiscence by pores is most perfect is endemic in tropical South America, as is also the highly interesting *Cochliostema*. In the Liliaceae and Amaryllidaceae, 4 of the 8 apically dehiscent genera are endemic in extratropical South America.

Thus, 11 of the 19 genera of the Monocotyledons are endemic in South America and another has 8 of its 10 species there.

Turning now to the Dicotyledons, we find that of the 40 genera, 11 are endemic in South America and 7 others occur there.

In the Monocotyledons, then, 57.8 per cent of the genera are endemic in South America, another has 8 of its 10 species there, while the two others may possibly have been derived from the same region; 63.1 per cent of the apically dehiscent monocotyledonous genera occur in South America. Among the Dicotyledons, we have 27.5 per cent endemic in South America and 7 more genera have some of their species, and in five cases the most of their species, in South America. Together, 18 of the 40 apically dehiscent genera of Dicotyledons are represented in South America, or 45 per cent.

Taking both Monocotyledons and Dicotyledons, we have 30 of the 59 genera assigned to this type represented in South America, or 50.8 per cent.

These genera contain from one to over nine hundred species; in some, all of the species are apically dehiscent, while in others, as in *Begonia* of about 400, and *Ardisia* of about 200 species, only a few species are apically dehiscent. To this question of the geographical distribution of species, we shall recur later. Here we may merely note that *Solanum* has about 700 of its 970 species in

South America, while *Cassia* has about 300 out of 412 in the same region.

In comparison with the above forms the distribution of the Melastomataceae is of great interest.

The family belongs to the tropical zone but is also represented in the subtropical, occurring between 30° N. and 40° S. Latitude. The family reaches its highest differentiation in tropical America where 6 (I, IV, V, VII, X, XI) of the tribes are exclusively found, 1 more (III) occurs in South America and extratropical North America, and another (XV) is found in tropical America, the Antilles, islands of the Pacific Ocean and tropical Africa. The other 7 are confined to the Old World. The tropical American tribes include 95 genera and three more are added by the two tribes of more general distribution while the single genus (*Rhexia*) in North America brings the number of American genera up to 99, with about 2,000 species all but 7 of which occur south of the United States (in this included the species of the Antilles) as compared with 62 genera with about 700 species from the remainder of the range. It is of interest to note that in the Memecyleae (Tribe XV), the only South American tribe occurring elsewhere, the dehiscence in the South American genus (*Olisbea* is by some regarded as merely a section of *Mouriria*) is by short slits which in many cases much resemble pores while in the other genera it is described as by longitudinal slits. Of this tribe there are 44 American and 101 Old World species. It will be noticed that in the tribes showing dehiscence by longitudinal slits (XII, XIV, XV) 2 genera with 44 species are American while 10 genera with 156 species are found elsewhere.

These figures are certainly suggestive, and seemed more so when it was found that the Apidae, the insects of the greatest importance in the fertilization of these forms, are strongly represented in South America, India and Austra-

lia. I resolved to carry out, so far as the nature of the data might permit, a statistical investigation of the problem.

At the present time, the importance of statistical methods is being emphasized by many writers. In floral ecology, attempts have long been made, and very successfully, too, in many cases, to estimate exactly the relative importance of each class of visitors in the evolution of a given flora. The problem at present in hand differs essentially from those which have preceded it in that it is an attempt to separate certain floral types and estimate their relative numerical importance in any flora.

The difficulties encountered are very great and the result obtained with the present material is not wholly complete. The following is the method employed and the results it has yielded.

The first requisite was the determination of the distribution of the apically dehiscent forms.

For the sake of convenience, the earth was divided into fourteen regions. It hardly need be remarked that in the present state of our knowledge any division into great and sharply defined phytogeographic regions is purely artificial and intended to serve merely as a convenience for further study. Fourteen divisions were recognized, since, after careful consideration, it seemed best to adopt so far as possible the floristic regions of Drude.

It was deemed best to have the regions represent, so far as possible, systematic rather than ecological units. It should be remembered that my own data had no influence in the selection of the divisions to be used. The principal need which led to the employment of a series of regions was the desirability of making a statistical comparison of the percentages of apically dehiscent genera belonging to the various types in the several floras. To facilitate tabulation, I have modified the regions as outlined by Drude by making their limits conform to geographical, or, in some cases, even political boundaries. Without this precaution,



it would hardly have been possible to gain any numerical idea of the relative frequency of the various forms as compared with the other members of the floras. These modifications have seemed perfectly justifiable in view of the purpose which the regions are to serve.

The divisions have been limited as follows: —

#### I. TROPICAL REGIONS.

1. TROPICAL AFRICAN REGION. Arabia and the continent of Africa south of the Tropic of Cancer to Cape Colony, South Bechuanaland, South African Republic, Basuto Land, and Cape Colony; also Sokotra Island.
2. EAST AFRICAN ISLAND REGION. a, Madagascar; b, Mascarine Islands and Rodrigues; c, Seychelles Islands.
3. INDIAN REGION. Western and eastern peninsulas of India and all islands lying between 17° N. lat. and the Tropic of Capricorn.
4. TROPICAL AMERICAN REGION. a, Brazil, Uruguay, Ecuador; b, Guiana, Venezuela, Colombia, Central America; c, Antilles and Bahamas; d, Mexico and Southern California.

#### II. AUSTRAL REGIONS.

5. SOUTH AFRICAN REGION. Continental South Africa south of the tropical region, and the island of St. Helena.
6. AUSTRALIAN REGION. Australia and Tasmania.
7. AUSTRAL AMERICAN REGION. Argentina, Chile, Patagonia and Tierra del Fuego.
8. NEW ZEALAND REGION. The island.
9. ANTARCTIC REGION. Land masses lying south of the above austral regions.

#### III. BOREAL REGIONS.

10. MEDITERRANEAN-ORIENTAL REGION. The Atlantic Islands (Canaries to Azores), Africa and Arabia north of the tropical region (Tropic of Cancer), Spain, Italy, Turkey in Europe and Asia, Transcaucasia, Persia, Baluchistan, Afghanistan, and the lands included by the outer limits of these.
11. CENTRAL ASIAN REGION. Turkestan, Mongolia and Tibet.
12. EAST ASIAN REGION. China, Manchuria, Korea, and Japan except Sakhalin Island.
13. CENTRAL NORTH AMERICAN REGION. Roughly commensurate with the United States.
14. NORTHERN REGION. Land masses of Europe, Asia and America above the limits of the four boreal subtropical regions described above.

It is evidently of great importance to ascertain just what per cent of the total number of plants known is to be found in each of these regions. The per cent of apically dehiscent forms occurring there can then be compared with this and it may be readily seen whether it is relatively greater or less than in other regions. A difference in the number of genera with a given floral habit in two floras which are being compared has little significance if the relative number of genera in the two floras varies in the same ratio. There must be some basis for comparison; the general conditions of life permit of a greater differentiation in some regions than in others of the same area and the extent of this differentiation must be known to serve as a basis for comparisons of the development of particular elements.

Being unable to find any suitable statement of the relative richness of the floras of different areas it became necessary to tabulate them especially for the present purpose. A comparison by species would probably be the most satisfactory, but it soon became evident that this presented too many difficulties. I therefore decided to tabulate the genera only and to take the data for this purpose from *Die Natürlichen Pflanzenfamilien*.

In the preparation of these tabulations the 8,541 genera of flowering plants were first set down in order followed by the numbers of the regions in which they occur. These were then summarized by families, the number of genera endemic and occurring in each region being indicated.

I present in Table A a summary of the distribution of all of the flowering plants arranged according to regions. In the first column is given the number of the several regions, in the second the number of endemic genera and the per cent which this is of the total number of genera of flowering plants, in the third column the number of genera occurring but not endemic, and in the fourth column the

total number of genera occurring and the per cent which this is of the whole number of plants.

TABLE A.

ALL GENERA OF FLOWERING PLANTS.

Region.	Endemic.	Others.	Total.
1	542 = 6.34%	1116	1658 = 19.41%
2	259 = 3.03%	579	838 = 9.81%
3	1126 = 13.18%	1344	2470 = 28.91%
4	1968 = 23.04%	1160	3128 = 36.62%
5	394 = 4.61%	468	862 = 10.09%
6	444 = 5.19%	712	1156 = 13.53%
7	175 = 2.04%	506	681 = 7.97%
8	23 = .27%	187	210 = 2.45%
9	4 = .04%	21	25 = .29%
10	455 = 5.32%	819	1274 = 14.91%
11	68 = .79%	549	617 = 7.22%
12	171 = 2.00%	846	1017 = 11.90%
13	335 = 3.92%	871	1206 = 14.12%
14	73 = .85%	654	727 = 8.51%

The second table, B, gives the number and the per cent of the 59 genera of the Solanum-Cassia type endemic and occurring in the several regions.

TABLE B.

GENERA OF SOLANUM-CASSIA TYPE. DISTRIBUTION.

Region.	Endemic.	Others.	Total.
1	2 = 3.38%	8	10 = 16.94%
2	1 = 1.69%	7	8 = 13.55%
3	7 = 11.86%	9	16 = 27.11%
4	17 = 28.81%	9	26 = 44.06%
5	2 = 3.38%	3	5 = 8.47%
6	12 = 20.33%	6	18 = 30.50%
7	4 = 6.77%	4	8 = 13.55%
8	.....	2	2 = 3.38%
9	.....	..	.....
10	.....	2	2 = 3.38%
11	.....	2	2 = 3.38%
12	1 = 1.69%	4	5 = 8.47%
13	.....	4	4 = 6.77%
14	.....	1	1 = 1.69%

A comparison of the per cents of this table with those of the one representing the distribution of all of the flowering plants is facilitated by subtracting the per cent of all genera in a region from the per cent of apically dehiscent forms and so indicating the relative abundance of the latter in plus and minus quantities, as in Table C.

TABLE C.  
GENERA OF SOLANUM-CASSIA TYPE. RELATIVE ABUNDANCE.

Region.	Endemic.	Total.
1	— 2.96	— 2.47
2	— 1.34	+ 3.74
3	— 1.32	— 1.80
4	+ 5.77	+ 7.44
5	— 1.23	— 1.62
6	+ 15.14	+ 16.97
7	+ 4.73	+ 5.58
8	— .27	+ .93
9	— .04	— .29
10	— 5.32	— 11.53
11	— .79	— 3.84
12	— .31	— 3.43
13	— 3.92	— 7.35
14	— .85	— 6.82

This reveals some suggestive points. In all regions except 4, 6 and 7, the per cent of apically dehiscent genera endemic is below that of all forms endemic in the same region. In all regions except 2, 4, 6, 7 and 8, the per cent of all apically dehiscent genera found is lower than that of other forms occurring in the same regions. In regions 4, 6 and 7, the average relative abundance of endemic apically dehiscent forms is 8.54 more than the average for the whole number of endemic forms while in the other eleven regions it is 1.66 less. For the apically dehiscent genera occurring in regions 4, 6 and 7 the average is 9.99 above while for the other eleven regions it is 3.22 below that of all genera occurring.

The great specific differentiation of *Solanum*, *Cassia* and

of many melastomataceous genera in tropical America first called my attention to the problem of the geographical distribution of these floral types.

It would appear that in general the most satisfactory statistical comparison of the floras of two or more regions is to be made not on the basis of genera but of species.

While this proposition would seem to hold for general comparisons of floras, we have in the present problem a special case in which the morphological differentiation of certain organs of the species entering into the composition of the floras rather than the taxonomic differentiation of the floras as a whole is to be considered. The comparison in this case should be based upon morphological rather than taxonomic units, but it becomes at once clear that it is quite impossible to separate the two conceptions.

I think that on the whole the special data which we seek are furnished by the characteristics of genera rather than by the peculiarities of species. In the limitations of the former, the floral organization has been assigned a more important place than in the separation of the latter where the vegetative features are usually more minutely studied and described. But even if all species of a genus have an identical floral structure it must not be forgotten that specific differentiation may permit of adaptation to more varied environmental conditions and so increase the relative importance of the genus as a constituent of the flora where the area under consideration is so large as to present a multiplicity of conditions.

In a comparison which embraces ecological considerations, as the present one does, there is one strong objection to taking the number of genera as data. In ecological comparisons, dominance is obviously of much significance. In floral ecology where the anthophilous fauna is the environment, one species may have characteristics which enable it to secure more visits than a dozen others. It is obviously incorrect to present merely a numerical statement of the

relative number of genera or even species represented in a region as indicative of the ecological conditions prevailing there. Only direct field observations of the fauna and flora will yield the exact data requisite for a satisfactory solution of the problem of the mutual interdependence of the distribution of floral structures and the organic environment to which they are adapted. Even these field studies cannot lay before us the past history of the species or structures in question and our knowledge must always lack the exactness of some other phases of biological investigation. These limitations notwithstanding, we should attempt to bring our knowledge to the greatest exactness possible. The broad outlines of a problem are often obscured for the naturalist in the field by the details of his observations and must be formulated by the worker in the herbarium and library.

I have been unwilling to forego an attempt at a comparison of the several regions by species. The difficulties in the way of such an undertaking are known only to those who have made a similar attempt. In the very beginning of the present study, it became evident that a comparison of the regions by per cents of the apically dehiscent species in the flora was quite out of the question, and even a comparison by genera, rough and unsatisfactory as it is, has required many months more than was originally anticipated.

The accompanying table, D, is a summary of the number of species of the *Solanum-Cassia* type occurring in each region and the per cent of the total number of apically dehiscent species of this type known, 1,827.

TABLE D.  
SPECIES OF THE SOLANUM-CASSIA TYPE.

Region.	Species.	Region.	Species.
1	107 = 5.85%	8	2 = .10%
2	42 = 2.29%	9	... ..
3	163 = 8.92%	10	40 = 2.18%
4	1142 = 62.50%	11	4 = .21%
5	37 = 2.02%	12	13 = .71%
6	186 = 10.18%	13	29 = 1.58%
7	100 = 5.47%	14	5 = .27%

This table shows that tropical America has 62.5 per cent of all the apically dehiscent species of the *Solanum*-*Cassia* type, the Indian region 8.9 per cent, the Australian region 10.1 per cent, the extratropical American region 5.47 per cent, while the other ten regions average but 1.52 per cent.

*Solanum* and *Cassia* comprise 1,382 of the 1,827 species of the foregoing tables. Anticipating the suggestion that the great differentiation of *Solanum* and *Cassia* in tropical America may account for the very high percentage of apically dehiscent species found there, I have given in Table E the distribution in numbers and per cents of all the apically dehiscent species except those of these two genera and, for comparison, have figured the per cents of these genera occurring in each region.

TABLE E.

SPECIES OF SOLANUM AND CASSIA COMPARED WITH OTHERS OF SAME TYPE.

Region.	Solanum.	Cassia.	Others.
1	5.98%	6.55%	22 = 4.94%
2	1.34%	2.43%	19 = 4.26%
3	7.22%	8.49%	59 = 13.25%
4	64.85%	70.39%	223 = 50.11%
5	2.68%	.73%	8 = 1.79%
6	5.36%	8.01%	101 = 22.69%
7	7.53%	4.13%	12 = 2.69%
8	.10%	.....	1 = .22%
9	.....	.....	... ..
10	2.66%	3.39%	... ..
11	.....	.31%	1 = .22%
12	.82%	.49%	3 = .67%
13	1.44%	2.67%	4 = .89%
14	.52%	.....	... ..

The similarity of these per cents is very striking, and, as it seems to me, significant.

For comparison with this I had selected at random from the indices of the several phanerogamous volumes of *Die Natürlichen Pflanzenfamilien*, 330 genera, the distribution of the species of these tabulated and the average number of species per genus in each region obtained. These averages are based upon too small a series to be of great value for comparison, but an estimate of the number of species for each region made on the basis of the number of genera occurring and the average number of species per genus, as shown by the sample selected, indicates that there is not the wide difference in the floras in general that is shown by the special forms under consideration.

The evidence from the *Solanum-Cassia* type seems clear and unmistakable. We may now apply this method of comparison to the two other floral types considered in this paper.

To the *Dilleniaceae* type have been assigned 16 genera



represented by 376 species, found in ten of the fourteen regions as indicated in Table F.

TABLE F.

## DILLENIACEOUS TYPE.

Region.	Genera.	Species.
1	4 = 25.00 %	14 = 3.72 %
2	2 = 12.50 %	15 = 3.99 %
3	10 = 62.50 %	220 = 58.50 %
4	6 = 37.50 %	75 = 19.95 %
5	1 = 6.25 %	3 = .77 %
6	6 = 37.50 %	22 = 5.85 %
7	1 = 6.25 %	7 = 1.86 %
8	2 = 12.50 %	6 = 1.60 %
11	3 = 18.75 %	8 = 2.13 %
12	3 = 18.75 %	6 = 1.60 %

It is unnecessary to compare the figures for this type with those for all plants. It will be seen that there is considerable similarity to the results obtained for the *Solanum-Cassia* type, but several points of difference may be in part due to the small number of genera and species assigned to this type.

The distribution of the Melastomataceae has already been considered in general terms. The distribution of the 152 genera assigned to the Melastomataceous type is shown in Table G.

TABLE G.

## GENERA OF MELASTOMATACEOUS TYPE.

Region.	Endemic.	Others.	Total.
1	13 = 8.55 %	6	19 = 12.50 %
2	8 = 5.26 %	2	10 = 6.57 %
3	22 = 14.47 %	9	31 = 20.39 %
4	96 = 63.15 %	1	97 = 63.81 %
5	3 = 1.97 %	1	4 = 2.63 %
6	.... .	4	4 = 2.63 %
12	.... .	6	6 = 3.94 %
13	1 = .65 %	0	1 = .65 %

These figures require no comment. The distribution of the species of the Melastomataceae, I have not figured. Cogniaux in his monograph of the family recognizes about 2,000 species from tropical America and 700 from Asia, Africa, Oceanica and Australia. The per cent of species in the fourth region is higher for this type than for any other, being roughly 73, while the remaining 27 per cent are found almost exclusively in the first, second and third regions.

Summarizing the distribution of the 227 apically dehiscent genera of all three types, we obtain the figures given in Table H.

TABLE H.  
SUMMATION OF GENERA, ALL TYPES.

Region.	Endemic.	Others.	Total.
1	16 = 7.04%	17	33 = 14.53%
2	9 = 3.96%	11	20 = 8.81%
3	34 = 14.97%	23	47 = 20.70%
4	116 = 51.10%	13	129 = 56.82%
5	5 = 2.20%	5	10 = 4.40%
6	13 = 5.72%	15	28 = 12.33%
7	4 = 1.76%	5	9 = 3.96%
8	....	4	4 = 1.76%
9	....	..	....
10	....	2	2 = .88%
11	....	5	5 = 2.20%
12	1 = .44%	13	14 = 6.16%
13	1 = .44%	4	5 = 2.20%
14	....	1	1 = .44%

#### THE GEOGRAPHICAL DISTRIBUTION OF THE APIDAE.

I was early impressed by the great number of Apidae, especially the larger species, occurring in South America. A preliminary tabulation of the tenth volume of Dalla Torre's Catalogus Hymenopterorum confirmed the impression derived from a casual examination of various special monographs, and the Apidae were then tabulated from this work according to the same regions as those used

for the plants. It hardly need be remarked that the regions recognized for the Apidae are identical with those used for the plants simply to facilitate comparison and not from any evidence derived from the classification or morphology of the former.

I present here in condensed form, in Tables I and J, a summary of the tabulations of the Apidae alone, and, by way of comparison, of all the genera of Hymenoptera (including Apidae) treated in Dalla Torre's voluminous work. These are arranged by regions in the same manner as the tabulations of the plants considered above.

To the Apidae belong 137 genera and to all Hymenoptera, including the Apidae, 2,407 genera.

TABLE I.  
GENERA OF APIDAE.

Region.	Endemic.	Others.	Total.
1	...	25	25 = 18.24 %
2	3 = 2.19 %	11	14 = 10.21 %
3	...	23	23 = 16.78 %
4	27 = 19.77 %	37	64 = 46.71 %
5	...	17	17 = 12.40 %
6	12 = 8.76 %	22	34 = 24.81 %
7	15 = 10.95 %	24	39 = 28.46 %
8	...	4	4 = 2.91 %
9	...	...	...
10	4 = 2.91 %	47	51 = 37.22 %
11	...	38	38 = 27.73 %
12	...	26	26 = 18.97 %
13	4 = 2.91 %	36	40 = 29.19 %
14	4 = 2.91 %	46	50 = 36.49 %

TABLE J.

ALL GENERA OF HYMENOPTERA.

Region.	Endemic.	Others.	Total.
1	44 = 1.82%	173	217 = 9.01%
2	7 = .29%	85	92 = 3.82%
3	120 = 4.98%	268	388 = 16.12%
4	283 = 11.75%	462	745 = 30.95%
5	10 = .41%	122	132 = 4.51%
6	50 = 2.07%	186	236 = 9.80%
7	40 = 1.66%	130	170 = 7.06%
8	6 = .24%	45	51 = 2.10%
9	...	...	...
10	125 = 5.19%	383	508 = 21.10%
11	14 = .58%	92	116 = 4.40%
12	29 = 1.20%	130	159 = 6.60%
13	210 = 8.72%	631	841 = 34.94%
14	699 = 29.04%	729	1428 = 59.30%

Expressing the distribution of the Apidae as compared with that of the Hymenoptera in plus and minus quantities, we have the accompanying table, K.

TABLE K.

GENERA OF APIDAE. RELATIVE ABUNDANCE.

Region.	Endemic.	Total.
1	— 1.82	+ 9.23
2	+ 1.90	+ 6.39
3	— 4.98	+ .66
4	+ 8.02	+ 15.76
5	— .41	+ 7.89
6	+ 6.69	+ 15.01
7	+ 9.29	+ 21.40
8	— .24	+ .81
9	...	...
10	— 2.28	+ 16.12
11	— .58	+ 23.33
12	— 1.20	+ 12.87
13	— 5.81	— 5.75
14	— 26.03	— 22.81

Regions 3, 4, 6 and 7 average  $+ 4.75$  for endemic genera, while the remaining nine regions from which Hymenoptera have been recorded average  $- 4.06$ . Turning to the total number of forms occurring in the several regions we find that 3, 4, 6 and 7 average  $+ 13.17$ , while the other nine regions average  $+ 5.28$ .

Conclusions concerning the distribution of the Hymenoptera must be only tentative since the vast order has been very little investigated, even in its most highly specialized family, the Apidae. The distribution by species need not be discussed in this place.

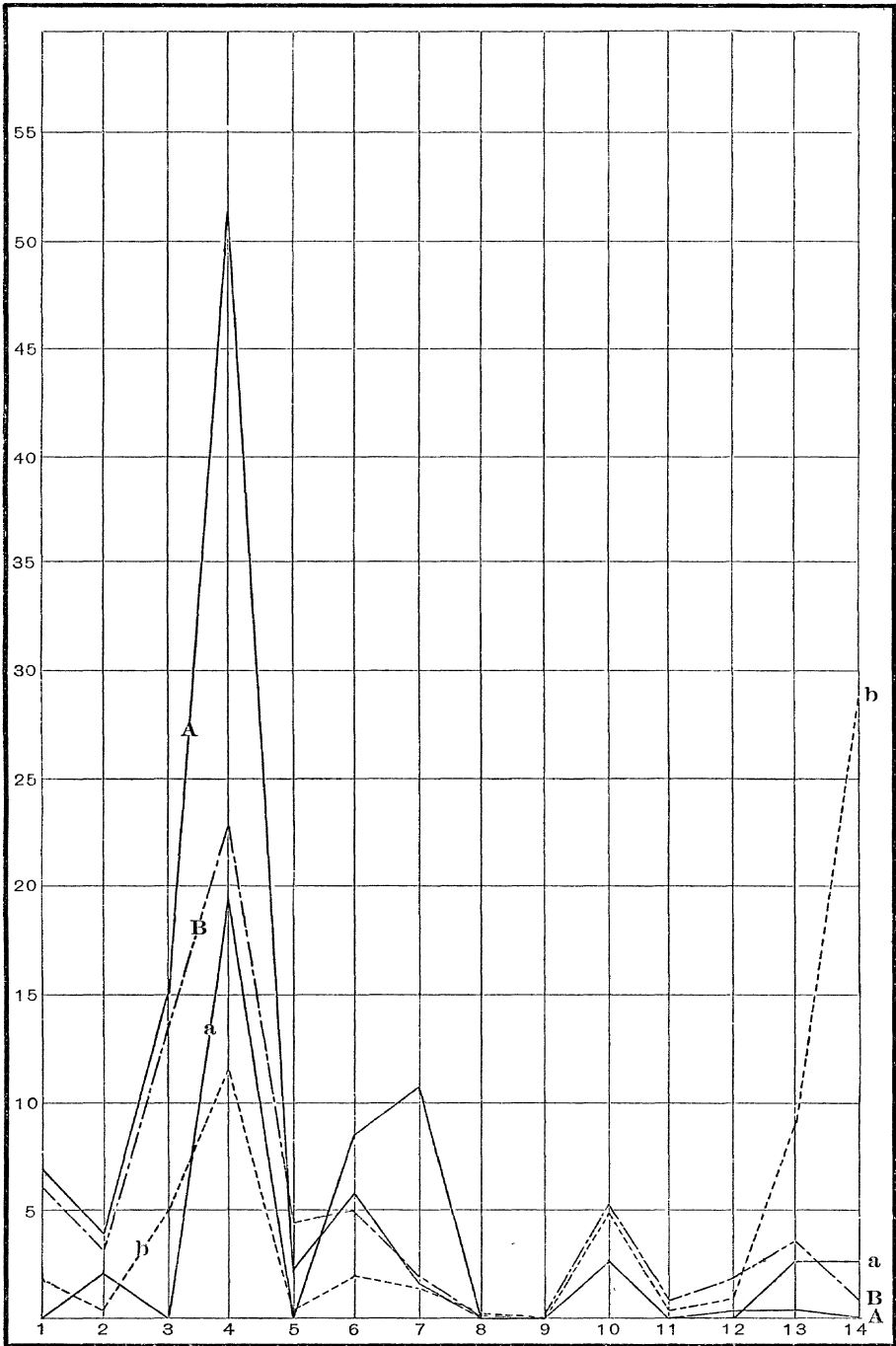
The points of agreement of these several tables are too apparent to need further comment. To facilitate comparison, the distribution of plants and insects has been summarized in the form of percentage curves. A glance at the accompanying diagrams, L and M, will make clear the relative proportion of the different elements in the flora and fauna and show the striking similarity between the distribution of the apically dehiscent genera and the Apidae. In this series of curves, the fourteen ordinates represent the fourteen regions, and the percentage of plants or insects endemic or occurring in a given region is indicated on these by the curves. A is the curve for the apically dehiscent forms, B for all genera; a for the Apidae, and b for all Hymenoptera. The high percentage of Apidae and other Hymenoptera in regions 10 to 14 is doubtless to be accounted for by the greater thoroughness with which these regions have been studied.

#### COMPARISON OF DISTRIBUTION OF FAUNA AND FLORA.

We seem to have in the data which have just been presented strong indications of a direct relation between the geographical distribution of the Apidae and that of the floral types which we have studied.

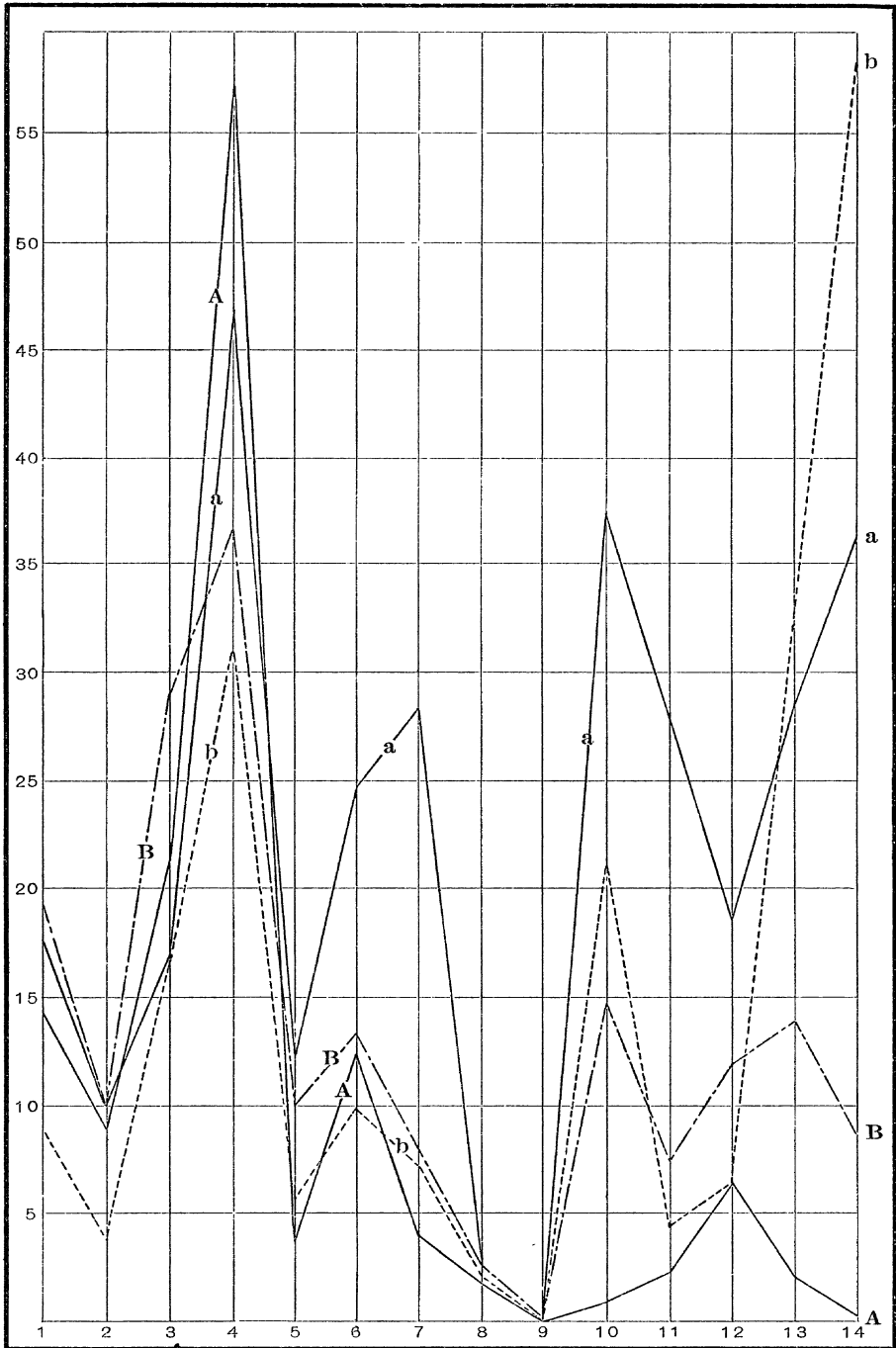
It is somewhat surprising that so little has been done towards the investigation of the distribution of floral

DIAGRAM L.



DISTRIBUTION OF ENDEMIC GENERA.

DIAGRAM M.



DISTRIBUTION OF ALL GENERA.

structures. The relation of flowers to insects is one of the oldest phases of ecology, and while Sprengel's beautiful observations of over a century ago were neglected until the theories and researches of Darwin and his contemporaries showed their importance, it was not long after the revival of interest in this fascinating branch of natural history that students began to see that if flowers show a reduced degree of fertility with their own pollen and are so closely adapted to some special visitor or group of visitors that others are unable to pollinate them, their geographical range will depend largely upon the distribution of the animals which are able to effect their pollination. That this phase of morphology and geography should have been neglected seems all the more remarkable in view of the significance assigned to floral structures in classification.

In the sixth chapter of his *Plant Geography*, Schimper considers animals as factors in plant distribution. Certain floral types, he considers, are undoubtedly limited in their geographical distribution by the range of the animals which pollinate them. The problem of adaptation for the protection of the plant from animal enemies has been much less satisfactorily investigated except in the case of myrmecophilism.

One of the best classes of data for the investigation of this problem is that furnished by ornithophilous flowers, since birds which are of importance as pollinators are of restricted range, and the adaptations, when they are real and not merely apparent, are evidently dependent in their range upon that of the organisms to which they are adapted. Comparatively few plants are ornithophilous, but the evidence offered is of such a character as to give us confidence in attacking the more difficult problem offered by entomophilous forms. Entomophily is the more general condition and in its geographical range is practically coextensive with the limits of the Phanerogams. Only three orders of insects seem to have influenced essentially the



structure of flowers, the Diptera, Lepidoptera and Hymenoptera. These groups are of general distribution, and species with flowers adapted to representatives of each of them may be found in almost every flora. The problem here is much more involved. Conclusions must, in this case, rest upon the demonstration of the interdependence of fauna and flora and statistical comparisons of the floras and faunas of different regions.

It is well known that the three orders of insects mentioned are represented in very different proportions in different regions, and the investigations of several workers have shown that there are corresponding differences in the constitution of the flora.

It is Hermann Müller to whom our knowledge of the influence of the insect fauna upon the constitution of the flora is largely due, for it was his contribution of the statistical methods of work which has made possible much which has been done since his time. So long as observations were confined to individual species showing adaptations to a single insect visitor or groups of visitors, conclusions were necessarily much limited and unsatisfactory. The development of methods which would permit of a statistical comparison of the adaptations of different flowers as a whole to insect visitors is clearly a step of fundamental importance, and, if the methods be trustworthy, permits of advances and conclusions of an accuracy otherwise quite unattainable, though the number of factors is so great and conditions are so complex that comparisons must remain only approximate.

In several papers, Müller developed various phases of the statistical methods, but it was in his book on Alpine flowers that he especially applied and illustrated these methods, and a review of the theoretical portion of this classic work will explain and illustrate the statistical method as developed by the German naturalist. Thomson, Loew, Warming, Lindman, Bonnier, MacLeod, Willis and Burkill, Knuth,

Robertson and others have made valuable contributions to this branch of statistical investigation.

The scope of this paper does not include a general review of the several attempts which have been made to demonstrate a relationship between the geographical distribution of flowers and the insect environment. MacLeod in the introduction to his careful investigation of the insect relations of the flowers of the Pyrenees has given such a review of the more important papers. Schimper and Drude have doubtless performed a great service for this phase of biological investigation by recognizing animals as representing one of the factors in physiological plant geography.

In this paper I have sought to approach the problem from a point of view different from that usually taken. Previous researches have been almost exclusively examinations of the range of individual species or genera which are clearly adapted exclusively to a single pollinating agent, with the range of the organism to which they are adapted, or statistical comparisons by the methods of Müller and MacLeod of floras of different regions, lowland and alpine, insular and continental, temperate and tropical and boreal.

I have tried to select all floral forms of a given type and after assuring myself of the reality of their morphological semblance and, so far as our limited knowledge of the plants in their living state would permit, of the similarity of their ecological relationships, I have considered their geographical distribution throughout the main divisions of the globe.

This method as applied to the problem of the morphology and biology of the apically dehiscent anther has yielded results which are, I think, of some importance in the larger problem of the evolution of floral structures.

Any problem in geographical distribution is necessarily dependent upon the validity of taxonomic or morphological

data, and writers who may speak with the greatest authority have repeatedly insisted that biogeographical researches are of the greatest value only when prosecuted by those who are deeply versed in the morphology and taxonomy of the forms treated. When the problem is one of physiological plant geography, and we have for consideration the additional factor of the environmental conditions and adaptations thereto, the problem becomes more complex. Upon the morphological and ecological data of the problem I have hardly touched in the present paper. I have sought, however, to carry out my comparisons with the greatest care, and I feel confident that the publication of the whole mass of evidence with all the exceptions to the more general laws and transgressions of the categories recognized would convince others of the validity of the propositions offered in this paper.

A point which will doubtless occur to all who examine into this phase of biology is that in the present work I have compared the morphology and geographical distribution of a single type of adaptation to a given factor,—believing that the *Solanum-Cassia* and *Melastomataceous* types may be considered as adapted to the peculiar habits of the *Apidae*, — with the form and distribution of all floral types, whether representing adaptations or not. For a final solution of the problem this method is obviously inadequate. It seems at first that the comparison should be confined to the entomophilous forms and that these should be segregated into their various types of adaptation for comparison; but the relation of all floral structures is one of such complexity that it seems that even this limitation of the field may be too narrowly drawn. Concurrence in both fauna and flora is here doubtless a factor of great importance, and far-reaching structural and field investigations must be made before the real relations will be finally made clear. In justification of the course which has been fol-

lowed in this study — if indeed any attempt at arrangement and interpretation of one class of data preliminary to the elaboration of all the material needs justification — it may be pointed out that these apically dehiscent types represent only two or three of the several types of flowers adapted to Apidae. Hypothetically all these types are well represented in regions which are rich in Apidae, and the relative values obtained for any type or types, as the *Solanum-Cassia* or *Melastomataceous*, would be too small rather than too large as an indication of the total influence of this factor of the environment, since the several types of adaptation to this factor, for instance the *Solanum-Cassia* and the *Verbascum* type among pollen flowers adapted to Apidae, will be in direct competition with each other as well as with all other types of adaptation.

Space has not permitted of the discussion of points of theory, such as the nature of the correlation between the different floral parts, the amount and nature of the influence of the fauna upon the evolution of these floral types, or the significance of these conclusions for current conceptions of floral evolution, nor would such be desirable in the absence of a more detailed presentation of the data upon which the conclusions actually drawn are based. In my final paper, I hope to point out the nature of some of these problems and to offer some suggestions as to the interpretation of the evidence already accumulated.

#### SUMMARY.

The three objects of the present investigation seem to be satisfactorily accomplished, and there only remains the working out of the large number of minor and detailed structural, ecological and geographical problems. A descriptive bibliographic list of apically dehiscent forms is nearly completed and the available material for a monographic treatment of their floral ecology brought together.

The work on the gross structure is being supplemented by a histological investigation of the anthers of the forms in question, and some hundreds of microscopical slides have been prepared and examined. Because of the great variety and in many cases complexity of structure this promises to be one of the most important phases of the work.

It has been shown that apically dehiscent forms for the most part fall into well defined categories exhibiting a striking uniformity of structure in genera or species from widely separated families. Structural parallelism in a series of floral forms assembled from phylogenetically widely separated groups necessarily implies the anomalous structure of many of the forms in the groups to which they systematically belong, among the forms to which they are genetically related. Of the real process by which this parallelism has been evolved I do not yet care to say anything. Many of the conclusions drawn from ecological studies are of little value because of the inadequacy of the data considered. Comparative researches attain their fullest value only when based on the largest series of material. At the present time, it seems to me, one of the most important things is to determine in how far floral organizations do really fall into well defined groups and in how far the structural characteristics of such groups may be regarded as adaptations. The first of these problems may be an herbarium and library investigation while the solution of the second is to be approached only by field studies.

Of the third and last problem little need be said. The tables presented show clearly that the apically dehiscent genera and species are not only much more abundant numerically in tropical America, Australia and the Indian region, but also that they form there a larger proportional constituent of the flora than they do in other regions. This distribution seems to depend in large measure upon the relative abundance of the Apidae in the several divisions.

So far as a biological science can be an exact science, plant geography and ecology must become exact sciences. One of the most promising methods of investigation, it seems to me, is to divide plant structure into classes limited as sharply and as naturally as possible, and to study the ecology and geographical distribution of these. When this is not done, the confusion of details is apt to obscure the results of the greatest value.